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CHROMOSOME STUDIES ON CALIFORNIA MOSSES

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CHROMOSOME STUDIES ON CALIFORNIA MOSSES

WILLIAM C. STEERE,[1] LEWIS E. ANDERSON AND VIRGINIA S. BRYAN

Introduction. The chromosomal behavior of bryophytes has been relatively little studied, compared with higher groups, perhaps because of the slight economic importance of these plants and the technical difficulties in making preparations for cytological research. A further impediment to cytological studies of bryophytes arises from the very considerable difficulty that may be experienced in identifying with certainty the species investigated. Outstanding exceptions, of course, were the first experimental production of polyploid series by the Marchals (1907, 1909, 1911), in mosses, and the first discovery of sex chromosomes in plants in an hepatic, *Sphaerocarpos,* by Allen (1917). The long-continued work of Allen (1945) on the genetics and cytology of *Sphaerocarpos,* the many brilliant experiments of Wettstein (1923, 1924, 1928, 1942) and his collaborators, (Barthelmess 1938, 1941) on apospory, hybridization, and genetics of mosses, and the recent comprehensive work of Burgeff (1943) on the genetics of *Marchantia* illustrate the richness of experimental material available among bryophytes.

The present investigation has had two principal aims: (1) to ascertain the chromosome numbers of native populations of Californian mosses, in order to relate these data to questions of phylogeny and taxonomy, insofar as possible, as Manton (1950) has done for pteridophytes, and (2) to study chromosomal behavior during meiosis, with emphasis on such criteria as the multiple association of chromosomes, premature and lagging disjunction, the so-called accessory chromosomes, sex chromosomes, and other phenomena that may influence the speciation and evolution of mosses. Careful studies of the meiotic process in mosses, with the aid of modern techniques, are very rare indeed. Notwithstanding the discovery of heterochromatin in mosses by Heitz (1928), and the investigation of meiosis in the Grimmiaceae (Vaarama 1949), many problems remain untouched and unsolved.

Early investigators of the chromosome behavior of mosses found the exact determination of chromosome numbers to be exceptionally difficult if not impossible, partly from the small size of the nuclei and partly from the characteristic tendency of the chromosomes to clump, thus apparently reducing their number (cf. Allen 1912, p. 123–128). The outstanding work of Heitz in developing new and more suitable techniques for the study of the nuclei of bryophytes enabled him (1928) to estimate the chromosome number of many mosses with reasonable accuracy, and later, to report with

[1] Grateful acknowledgment is made to the National Science Foundation for a grant of research funds to Stanford University (NSF-G186) which has not only made the present investigation possible, but will enable it to be continued.

some certainty the chromosome numbers of several further species (1932, 1942). Since the pioneer efforts of Heitz (1926, 1928), reports of chromosome studies of wild populations of mosses have appeared with increasing frequency, among which the most important are those by Jachimsky (1935), Kurita (1937, 1939), Lowry (1948), Shimotomai and Kimura (1936), Shimotomai and Koyama (1932), Sinoir (1952), Tatuno (1951), Yano (1951, 1952), and especially the recent and exceptionally important works of Vaarama (1949, 1950a, b, 1953a, b). At the present time, the chromosome number of about 150 species of mosses has been reported, with varying degrees of accuracy, out of approximately 20,000 species that have been described. Tabular summaries of published chromosome numbers have appeared recently in the works of Lowry (1948) and Sinoir (1952). Except for scattered earlier works, for example those of Allen (1912) on *Polytrichum juniperinum,* and of Scheuber (1932) on *Timmia cucullata,* most of the chromosomal studies on North American mosses have been made very recently, especially by Lowry (1948, 1953) and by Vaarama (1949, 1950b, 1953a, b). The total number of species whose chromosome number has been reported from American material perhaps reaches 25 and certainly does not exceed 30. Consequently, the present investigations, covering the behavior of meiotic chromosomes in 55 species, have doubled the number of American species so far studied. We are able to report chromosome numbers and behavior in 2 families, 15 genera, 37 species, and 7 varieties whose chromosomes have not been studied previously, as well as in 7 species that had been investigated earlier, primarily in European populations. The emphasis of the great majority of the investigators just cited has been on problems concerned with heterochromatin, sex chromosomes, and on chromosome number for its own sake. The only serious attempt to correlate chromosome numbers and behavior with the taxonomy of mosses is that of Lowry (1948), in his thorough cytotaxonomic investigation of the genus *Mnium.* In view of the relatively restricted attention paid to the use of cytological data in systematic problems in mosses in the past, and with a very considerable further body of new data available from our investigations, the time seems appropriate for an analysis of previously reported chromosome counts with special reference to their bearing on problems of phylogeny and taxonomy.

Materials. Admittedly, the choice of Californian mosses as material for this investigation was determined largely by the residence of the senior author. Nevertheless, the Californian moss flora presents several advantages for such studies, among them the facts that it is a rich and interesting one, consisting of over 300 species (Koch 1950) ; that many species become conspicuously abundant under favorable conditions; that it presents a good deal of significance in the families and genera that comprise it, in terms of

patterns of geographic distribution and floristic migrations (Lesquereux) 1865, 1868); and that most species produce their sporophytes and undergo meiosis during a few months in winter and spring, thus insuring abundant experimental material during the proper season.

One of the most troublesome problems encountered in this investigation was identification of the species with some degree of certainty. The standard practice of applying European names to many species of North American bryophytes is open to considerable doubt and suspicion, because of the clear differentiation of the floras of the two continents (Fernald 1931). Furthermore, the names of species of the eastern United States are too often applied to populations of the West Coast that appear to be specifically distinct. Of course, the corollary is true: significant chromosomal differences between populations of Europe or of the Eastern United States and those of the West Coast may prove to be very helpful in clarifying taxonomic problems.

Material of more than 60 species and varieties, not all of which yielded preparations suitable for cytological study, was collected in the general vicinity of San Francisco Bay, in Santa Clara, San Mateo, Santa Cruz, Marin, and Contra Costa counties. A few collections came from as far north as Sonoma County, at the Hedgpeth Ranch, and Mendocino County, at Ukiah. Some further collections were obtained in the Sierra Nevada, in Yosemite National Park, Mariposa County.

Each population studied cytologically is represented by a voucher specimen deposited in the Dudley Herbarium of Stanford University. These specimens, each referred to in the following report by the initials of the author who collected it and numbered in a consecutive series, will furnish a permanent record of our species concepts and identifications (cf. Sauer 1953), and the detailed locality data will make possible the recovery of the populations at any time. In the absence of permanent cytological preparations, this sort of documentation may prove useful to others working on the chromosomes of mosses, especially if they wish to duplicate our results.

Methods. As the technical difficulties in studying the chromosomes of bryophytes have presented one of the greatest handicaps to research in this field in the past, the methods used in the present investigation will be outlined in some detail. When mastered, the techniques are relatively easy, and thereby open to investigation a group of plants that have remained too long neglected.

At meiosis in the spore mother cells (SMC) or sporocytes of mosses, the chromosomes are especially satisfactory for determination of their number. During the meiotic divisions the chromosomes tend to be greatly condensed, deeply staining and, in the early stages, conjugated in pairs, presenting the reduced number in a compact, easily-resolved state.

A further advantage of the dividing SMC is the correlation that usually exists between the stage of its development and the external appearance of the sporophyte. Maturing sporophytes of a few species can be found throughout the year in some regions of the United States, although in California, most species produce capsules only during the winter and early spring months. At the time of meiosis sporophytes are characterized by their bright green appearance and by their attainment of mature size. Mosses collected when the capsules are approaching mature size will continue normal development if kept in a cool laboratory with diffuse sunlight, in covered glass dishes or in plastic bags. A large collection was made whenever possible since the capsules within a population may represent a wide range of development. A collection that includes dark green or brown mature capsules, and also completely green capsules of mature size, will almost certainly contain all the meiotic stages.

The best chromosome preparations are made as soon as possible after collecting mosses in active metabolic condition. Plants collected under conditions of excessive cold or dryness, however, usually give better results if watered and stored in the laboratory for several hours to several days. When most of their capsules appear to be near the meiotic division mosses may be stored in a refrigerator, where the reduced temperature will arrest or delay the development of the sporophyte and maintain the plants in good condition until they can be studied, especially if supplied with light for several hours each day.

For squash preparations, the most promising capsules are selected under the binocular dissecting microscope. As a general rule meiosis occurs when the capsule is mature in form and size, but still green and slightly translucent; the cells of the annulus may show some brown or red coloration and the operculum may be tan. However, in some species the SMC divide when the entire capsule is bright green and in others when the capsule wall itself has become mostly red-brown.

The capsule, severed from the seta, is transferred to clean slide. Under a binocular dissecting microscope the operculum is removed with a fine needle or spear, and pressure applied at the base of the capsule. In most species the contents of the capsule can be squeezed out; in others, the spore-bearing tissues must be dissected out.

A saturated solution of orcein in 45 per cent acetic acid (acetic orcein) gives adequte fixation in many species, but not in all. The solution itself or the weight of the cover slip on inadequately fixed cells may cause the SMC to disintegrate. Preliminary fixation in Carnoy's solution is advisable as a precaution in the preparation of squashes of moss capsules. A drop of fixative is added as soon as the SMC are removed from the capsule and care must be taken to prevent the SMC from drying. Any Carnoy-type fixing

solution (3:1; 3:6:1; 4:3:1) may be used and little difference will be noted in the resultant preparations.

A second and even a third drop of fixative may be required for delicate cells or those with large obscuring inclusions.

An acetic-orcein staining solution, prepared by adding 1.5 gm. of orcein (National Aniline synthetic) to 100 cc. of 45 per cent acetic acid and shaking until the solution is saturated, gives excellent results with moss chromosomes. After filtration this solution produces an intense stain in the chromatin but is taken up only slightly by the cytoplasm. Periodic filtrations may be necessary to remove a fine iridescent precipitate. Natural orcein gave a less intense stain than the synthetic dye. A drop of aceto-orcein is added when the fixative has almost entirely evaporated and a cover slip placed over the stain. Heating the slide almost to the boiling point over a small flame intensifies the stain in the chromosomes and clears the cytoplasm. Following the heating process, the slide should be checked under the microscope to determine in a general way the condition of the cells. Stages with spores or with SMC that are obviously too young may then be discarded without further treatment. An attempt should then be made to distribute the cells in a single layer between the slide and the cover slip. When the slide is re-heated and placed on a flat surface, repeated gentle tapping on the cover glass with the handle of a dissecting needle causes the cells to flow apart into one layer. The progress of this operation may be checked with the compound microscope, under low power, and the pressure of the tapping decreased or increased as the fragility of the cells indicates. The slide, re-heated, is inverted on absorbent paper when the cells are well spread; gentle pressure at the edges will force out surplus stain. If the cells were still intact, pressure may be applied over the cover slip itself to flatten the preparation further.

Since capsules with early tetrad stages sometimes include a few cells with earlier stages, they are occasionally useful for estimates or for verifications of chromosome numbers. In preparations including cells in which cytokinesis has started, the flattening of metaphase figures is likely to be difficult. Cells in early prophase are sometimes accompanied by a few prematurely dividing SMC that may furnish first metaphase counts. Diakinesis figures are helpful in obtaining counts in species whose chromosomes tend to clump at first metaphase and for verifying the presence of accessory chromosomes or fragments. Naturally, the most useful preparations include stages from late prophase through second anaphase.

When the metaphase chromosomes do not stain intensely, more stain should be added and the preparation re-heated. The chromosomes of most mosses stain sufficiently for study immediately but some preparations may need to stand for a few hours.

To seal the completed preparations, the slide is warmed and vaseline drawn around the edge of the cover slip with a needle. By heating gently the vaseline will flow around the edge of the cover glass. Temporary mounts remain in good condition for at least one day, ample time for the study of the SMC of one capsule. If necessary, storage in a damp chamber at a reduced temperature will preserve the preparations longer.

Certain hazards exist in the interpretation of the division figures. In cells which have been strongly flattened, first anaphase or second metaphase plates may flow together and appear as a single figure. The tendency for homologous chromosomes to separate precociously in meiosis of mosses, observed previously by Vaarama (1949), may give an erroneous impression of aneuploidy or polyploidy. Similarly, chromatids anticipating the next division may be observed as early as first metaphase in some species. The secondary association of bivalents at first metaphase, discovered in our investigations, may lead to the appearance of fewer chromosomes in the first metaphase plate than in the succeeding stages.

The number of chromosomes is best ascertained through the study of many figures at diakinesis, metaphase I and anaphase II. Otherwise, several possible anomalies of meiosis, as the multiple association of bivalents, their premature dissociation, the premature division of anaphase chromosomes, the lumping of chromosomes at any stage, or the presence of polyploid areas in the archesporium, may result in an incorrect chromosome count if a single stage of meiosis is observed. The authors generally studied as many meiotic stages as possible in as many sporocytes as could be found in suitable condition in each population.

All three investigators made separate chromosome counts of each population reported upon here. When these independent studies were not in agreement, observations were continued until the differences in opinion could be reconciled. If unanimous agreement could not be reached on the basis of the available material of some populations, no report has been included here. All drawings have been made (largely by the senior author) to the same scale, under standard conditions, with the aid of a 1.4 mm. oil immersion lens, a 20 × compensating ocular, and a camera lucida. The magnification achieved with this equipment, in all drawings (figs. 1–183, is × 2800. The magnification of all the published drawings is × 2160.

Results. Our data will be reported under the heading of the various families to which the populations belong, arranged in the order established by Brotherus (1924–1925). Insofar as possible, our results are coordinated with those of previous workers, for the sake of completeness. A brief summary of the results, with some interpretation, is given at the end of each family.

FISSIDENTACEAE

Fissidens (*Bryoidium*) *limbatus* Sull. (figs. 1–4): $n = 5$. This count is of especial interest for two reasons, for the small number of chromosomes, and also because this number does not seem to be related closely to any series of chromosome numbers reported for other species of *Fissidens,* here or elsewhere. The meiotic chromosomes of *F. limbatus* are very similar in size and shape and behave regularly in both divisions. As seems to be not uncommon in mosses, but more conspicuous here than in most species, the bivalent chromosomes tend to dissociate prematurely, producing 10 univalents at the first metaphase (figs. 3 and 4). This species is a common and variable one, occurring on moist shaded soil, especially on vertical banks, where it is usually one of the first plants to appear. The population studied here grows on the east bank of San Francisquito Creek, Santa Clara County, at the Stanford University Golf Course (LEA 1, Feb. 10, 1953).

Fissidens (*Aloma*) *pauperculus* Howe (figs. 5–7): $n = 12$. This extremely rare and local species has remained almost completely unknown until its rediscovery a few years ago (Koch 1948), and still seems to be restricted in its geographical distribution to the range of the coast redwood, *Sequoia sempervirens* (Koch 1951). The chromosome complement differs markedly from that of *F. limbatus,* not only in number, but also in morphology, since the chromosomes of the present species fall very clearly into several size and shape classes. The premature dissociation of a single bivalent before the first division provides a further feature of interest in the chromosome behavior at meiosis. Our material came from the slopes of Mt. Tamalpais in Marin County, near the Muir Woods National Monument, from bare soil at the very base of a coast redwood (LEA 53, April 8, 1953).

Summary. The Fissidentaceae, consisting almost entirely of one very large genus, presents one of the finest assemblages of material for cytotaxonomic study available among mosses. The genus *Fissidens*, with nearly a thousand described species, occurs abundantly in all parts of the world, although not as richly in California and the West Coast in general as in most other parts of the United States. Towards the tropics, the species of this family become progressively more numerous. The grouping of the species of *Fissidens* presents some interesting problems. Grout (1943), in the most recent monograph of the North American species, recognizes eleven sections. Other authors consider that some sections actually deserve the categorical rank of subgenera, and they may be raised eventually to the status of independent genera (Steere 1947), especially if cytotaxonomic evidence supports such a change in concept. However, a surprisingly small number of species have had chromosome counts reported, and none of them from American populations. On the basis of European material, Heitz (1928) reported that *Fissidens adiantoides* Hedw. has "(19)21" chromosomes, and

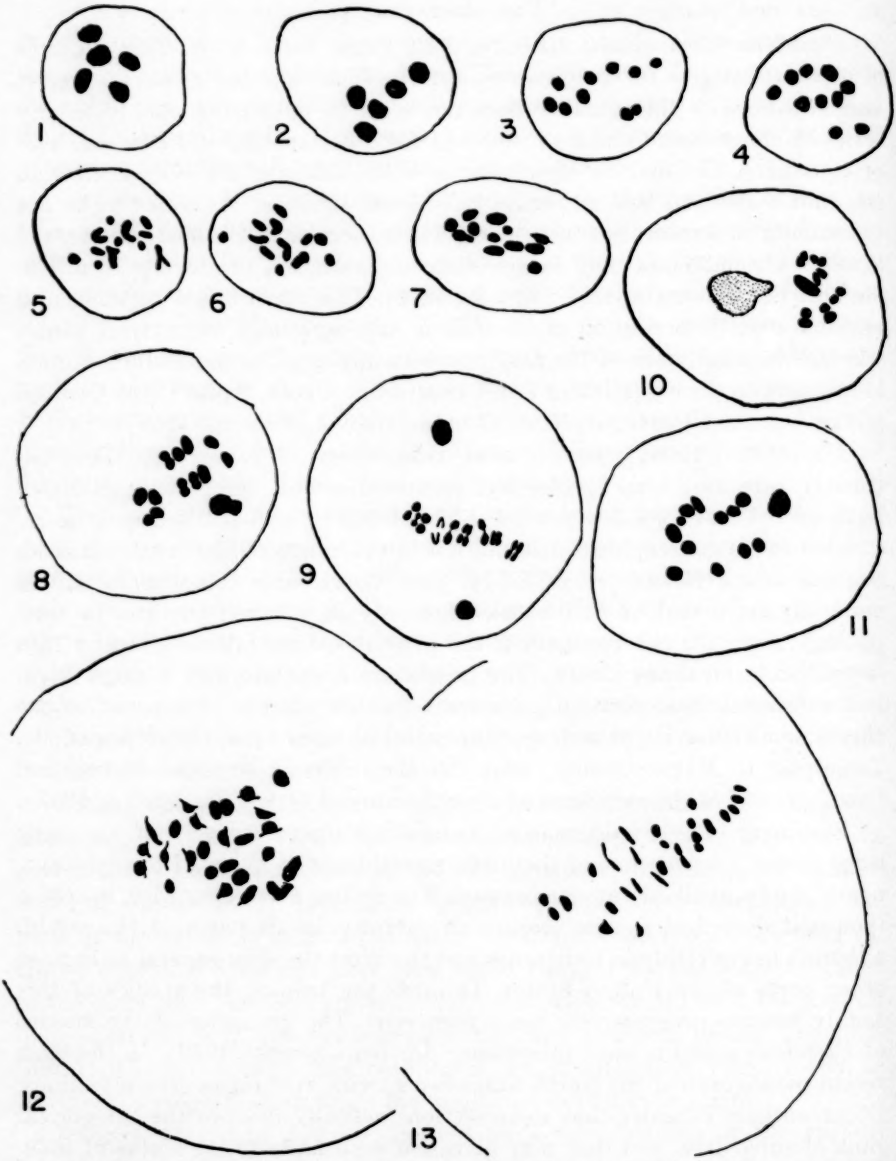

PLATE I. FIGS. 1–4. *Fissidens limbatus* ($n=5$). FIGS. 1 and 2. Polar views of first metaphase, with five bivalents. FIGS. 3 and 4. Sporocytes in which all bivalents have dissociated precociously. FIGS. 5–7. *Fissidens pauperculus* ($n=12$). FIGS. 5 and 6. Bivalent chromosomes just before first meiotic metaphase. FIG. 7. Polar view of first metaphase. FIGS. 8–10. *Ceratodon purpureus* ($n=13$). FIG. 8. First metaphase, early. FIG. 9. First anaphase, early. FIG. 10. First telophase, one chromosome group consolidated. FIG. 11. *Ceratodon purpureus* fo. *xanthopus* ($n=13$), polar view of first metaphase. FIGS. 12 and 13. *Ditrichum schimperi* ($n=26$). FIG. 12. Polar view of first metaphase, early. FIG. 13. Side view of first metaphase. All figures × 2160.

Sinoir (1952) very recently indicated that in *F. taxifolius* Hedw., $n = 9$. By coincidence, these species belong to the same section, Sect. *Serridium,* and are reasonably closely related. Yano (1951) has reported the number, $n = 16$, for *F. cristatus* and *F. japonicus.* Fortunately for our survey of sections, the two Californian species studied represent two further sections, Sect. *Bryoidium* and Sect. *Aloma.* It is interesting to note that the sections so far studied possess very different chromosome complements, although it is still too early to draw any serious conclusions on the significance of this fact.

DITRICHACEAE

Ceratodon purpureus (Hedw.) Brid. (figs. 8–10) : $n = 13$. Our findings, the first to be based on American populations, agree with previous reports on European material, even to the presence of a bivalent that is much larger and more conspicuous than the others. The association of bivalents at and just before the first meiotic metaphase, as well as their appearance of duplication (fig. 8), would seem to furnish evidence that this is a polyploid species in terms of the autosomes and that the much larger "bivalent" may perhaps represent a multivalent structure. A careful and detailed study of the prophase stages of meiosis, as well as of the gametophytic chromosomes of this species would be well merited, to obtain further information concerning these points. Our material of this common and weedy species came from a sandy roadside at the upper entrance to Big Basin State Park, Santa Cruz County (WCS 43, March 18, 1953). A further check was made on material from Yosemite National Park, Mariposa County (VSB, 55, April 5, 1953).

Ceratodon purpureus (Hedw.) Brid. fo. *xanthopus* (Sull.) Britt. (fig. 11) : $n = 13$. Originally described in the category of a variety, this geographical race is very common in California, and differs from the species by its longer seta which is yellow rather than red. We found no significant difference between the chromosomes of this form and of the species, at least in our preliminary studies. The material investigated came from a roadside cliff in Marin County, between Tomales and Petaluma (WCS 57, April 11, 1953).

Ditrichum schimperi (Lesq.) Paris (figs. 12 and 13) : $n = 26$. No chromosome numbers for this genus have been reported previously. The well-recognized relationships of *Ditrichum* to *Ceratodon* may be reflected by the closely related chromosome numbers, even though the appearance of the chromosome complement is very different, indeed. Several classes of chromosome size and shape may be distinguished, but the single, very much larger bivalent so characteristic of *Ceratodon* is lacking, at least in this species. Three chromosome pairs tend to be so closely associated before the first meiotic division that occasional counts, $n = 24$, were made, until this anom-

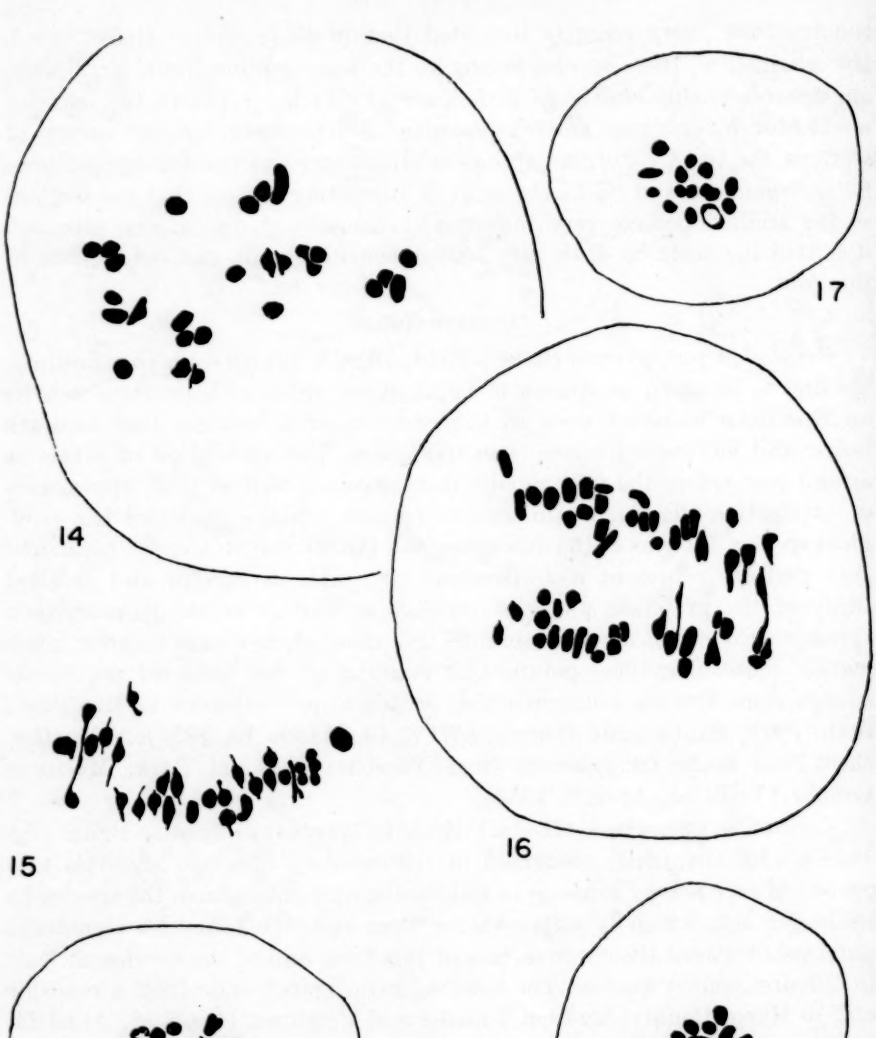

PLATE II. FIGS. 14–16. *Pleuridium bolanderi* ($n = 26$). FIG. 14. Polar view of first metaphase, early. FIG. 15. Side view of first metaphase. FIG. 16. First meiotic anaphase. FIGS. 17–19. *Anisothecium varium* ($n = 14$), polar views of first meiotic metaphase showing behavior of "accessory" chromosomes. All figures $\times 2160$.

alous behavior was understood. The population studied occurs on soil under redwoods, Mt. Tamalpais, just above Muir Woods National Monument (LEA 59, April 8, 1953).

Pleuridium bolanderi C. Müll. (figs. 14–16) : $n = 26$. This appears to be the first chromosome count reported for the genus. The behavior of the chromosomes at meiosis is such that an accurate count was very difficult to achieve, since bivalent and univalent chromosomes may not always be distinguished easily on the basis of size alone. As a result of differences in the time of disjunction of the different chromosome pairs, counts ranging from 26 to 30 chromosomes were made. However, a few very clear preparations of spore mother cells just prior to the first meiotic metaphase show definitely that 26 is the basic number and that any number over this represents disjoined pairs rather than bivalents. Diakinetic figures in this material showed chiasmata distribution with unusual clarity. The population studied was collected near Pepperwood Creek, on the Hedgpeth Ranch in western Sonoma County (WCS 12, Feb. 22, 1953).

Summary. Until now, only one genus and species of the Ditrichaceae has been studied cytologically although the family contains nearly 20 genera. *Ceratodon purpureus* has received an unusual amount of attention, partly because of its great abundance and wide distribution in the northern hemisphere, and partly because of its remarkable chromosome complement, which includes a very large "sex" chromosome. This species has been studied by Heitz (1928), who reported the chromosome number, $n = 11–12$, and by Jachimsky (1935), Shimotomai and Kimura (1936), and Vaarama (1950b), all of whom reported that $n = 13$. Although it may eventually turn out to be in part only a coincidence, it is interesting to note at this point that in the three genera of Ditrichaceae so far studied, the basic haploid chromosome number is 13.

Dicranaceae

Anisothecium varium (Hedw.) Mitt. (*Dicranella varia* Schimp.) (figs. 17–19) : $n = 14$. This is the first species of a relatively large genus to have its chromosome behavior investigated. A feature of unusual interest is found in the closed (fig. 17) or open (figs. 18–19) ring of 4 very small chromosomes, of the type that Vaarama has called accessory chromosomes. Since these are usually associated, they are considered here as one bivalent chromosome that has undergone premature division. This is a situation where the study of somatic chromosomes would be especially enlightening as a means of showing the relationship between mitotic and meiotic chromosome behavior, something at present very little understood in mosses. The material was collected from a population growing on the steep east bank of San Francisquito Creek, at the Stanford University Golf Course, Santa Clara County (LEA 2, Feb. 10, 1953).

Dicranoweisia cirrata (Hedw.) Lindb. (figs. 20–22): $n = 11$. This count, observed in many sporocytes, seems to be beyond reasonable doubt. One figure, at a late diakinesis stage (fig. 20), seems especially conclusive. The meiotic chromosomes fall into several distinct size classes, with four large pairs, of which one is dimorphic, three pairs of medium size, three small pairs, and one pair so small that it might well be classed in the category of accessory chromosomes, were it not for the very regular pairing and the presence of other chromosomes almost as small. Although no other chromosome counts have been made in this genus, the number reported here fits well within the chromosome range known for the family. The material investigated came from the fire-scarred base of a large redwood at Big Basin State Park, Santa Cruz County (WCS 31, March 18, 1953).

Summary. The Dicranaceae, a large and interesting family consisting of some 50 genera, have received very little chromosome study, and chromosome counts have been reported earlier from only four genera. Heitz (1928) reported the number, n = ca.12, for *Rhabdoweissia fugax;* Vaarama (1950b) has studied *Cynodontium strumiferum* ($n = 15$) and *Paraleucobryum longifolium* ($n = 12$); and several species of *Dicranum* have been investigated by various workers, giving chromosome counts of $n = 10$–12 (Heitz 1928, Shimotomai & Koyama 1932, Vaarama 1950a, b, Yano 1951). The chromosome numbers of these six rather unrelated genera, although representing a rather small percentage of the family, nevertheless would seem to indicate that low chromosome numbers may be expected throughout.

Encalyptaceae

Encalypta vulgaris Hedw. var. *mutica* Brid. (figs. 23–25): $n = 13$. From the relatively large size of the sporocytes, among the largest found in this investigation, and from the well spread out chromosomes, there could be no doubt about the number reported here. A point of cytological interest is the distinctive shape and size of several of the bivalent chromosomes, especially one that is clearly dimorphic. The regular behavior of the chromosomes in meiosis gives no clue to the extensive and widely recognized variability of this species. The population studied grows on the north slope of Mt. Hamilton, Santa Clara County, on bare soil in chaparral vegetation (WCS 39, March 24, 1953).

Summary. The Encalyptaceae consisted of the single genus, *Encalypta,* with about 30 species, until recently, when the previously incompletely known genus, *Bryobrittonia,* was discovered to belong here (Steere 1953). No chromosome numbers are previously reported for members of this family. The systematic position of the Encalyptaceae has been the source of some debate, because of the unusual range of variation in the structure of the peristome, which, depending on the species, may be lacking, single, or

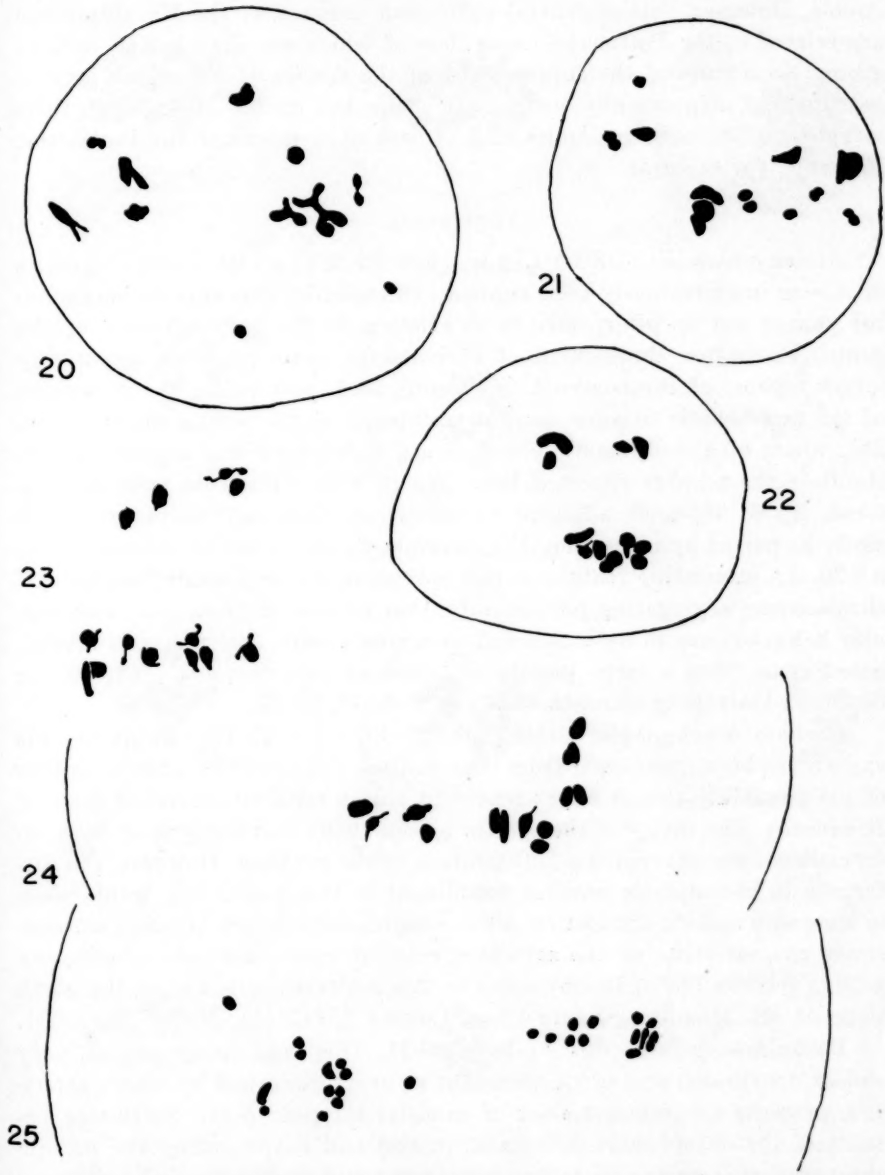

PLATE III. FIGS. 20–22. *Dicranoweisia cirrata* ($n=11$). FIG. 20. Sporocyte at diakinesis. FIG. 21. First metaphase, early. FIG. 22. First metaphase, polar view. FIGS. 23–25. *Encalypta vulgaris* var. *mutica* ($n=13$). FIGS. 23 and 24. Side views of first meiotic metaphase. FIG. 25. Polar view of second metaphase. All figures $\times 2160$.

double. However, rather general agreement exists that the Encalyptaceae are related to the Pottiaceae, regardless of which one may be the derived group. No feature of the chromosomes of the species of *Encalypta* investigated would disprove any such relationship, but on the other hand, their morphology strongly resembles that of several members of the Pottiaceae, *Phascum*, for example.

Pottiaceae

Aloina ambiguua (BSG.) Limpr. (figs. 26–28) : $n = 24$. Since no species of *Aloina* has previously been studied cytologically, this chromosome number cannot yet be interpreted with relation to the cytotaxonomy of the genus. Premature disjunction of chromosome pairs gives an apparently larger number of chromosomes, but counts made just before the metaphase of the first meiotic division, and at metaphase of the second division (fig. 28), where all the chromatic elements are visible and well separated, substantiate the number reported here. Where higher numbers were encountered, up to 30, some adjacent chromosomes, obviously univalent, could easily be paired by inspection. For example, figure 27 can be interpreted as $n = 26$. An interesting feature of this species is the very small "accessory" chromosomes segregating prematurely, that because of their otherwise regular behavior, are to be considered as a single pair. The material investigated came from a large population growing near Sequoia Hall, on the Stanford University Campus (LEA 6, Feb. 19, 1953).

Barbula brachyphylla Sull. (figs. 29–30) : $n = 12$. The status of this species has been questioned from time to time (Steere 1938, 1939), because of the possibility that it might represent only a reduced ecological form of *B. vinealis*. The rarity of the species (Koch 1950) and the lack of field observations have prevented a full solution of the problem. However, the difference in chromosome number established in this population would seem to suggest a specific distinction. Two conspicuously larger bivalent chromosomes characteristic of the several species of genus *Barbula* (Jachimsky 1935, Vaarama 1950a, 1953b) occur in this material, collected on the north slope of Mt. Hamilton, Santa Clara County (WCS 45, March 26, 1953).

Barbula convoluta (figs. 31–32) : $n = 11$. This semi-weedy species, very widely distributed and often abundant in areas disturbed by man's activities, presents a chromosome set of unusual interest in the Pottiaceae because of the conspicuous differences in size and shape among the meiotic chromosomes. In addition to two large pairs and one very small pair there is a bivalent clearly dimorphic in side view. This chromosome number does not agree well with that reported for other members of the genus *Barbula*. As more species are studied, it will be of interest to determine if the different sections of the genus, some of which have themselves been raised to

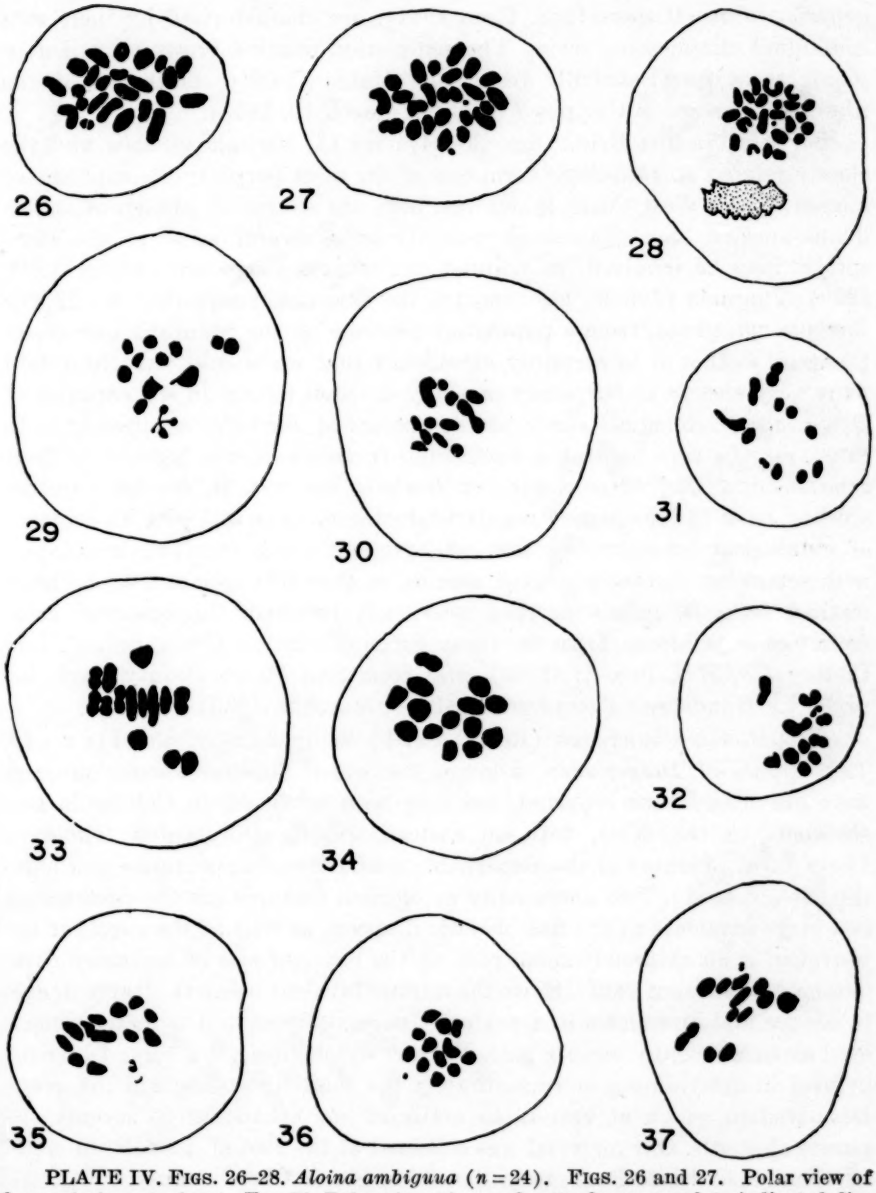

PLATE IV. FIGS. 26–28. *Aloina ambiguua* ($n = 24$). FIGS. 26 and 27. Polar view of first meiotic metaphase. FIG. 28. Polar view of second metaphase, one plate indicated diagrammatically in side view. FIGS. 29 and 30. *Barbula brachyphylla* ($n = 12$). FIGS. 29 and 30. First meiotic metaphase, early and median, respectively. FIGS. 31 and 32. *Barbula convoluta* ($n = 11$), polar views of first metaphase. FIGS. 33–34. *Barbula vinealis* ($n = 14$). FIG. 33. Early metaphase, first division. FIG. 34. Polar view of first metaphase. FIGS. 35–37. *Desmatodon hendersonii* ($n = 13$), polar views of first meiotic metaphase, showing "accessory" chromosome. All figures $\times 2160$.

generic status (Hilpert 1933, Chen 1941), are characterized by their own individual chromosome series. The population studied grows on soil at a picnic area near Searsville Lake, San Mateo County, southwest of the Stanford University Campus (WCS 36, March 10, 1953).

Barbula vinealis Brid. (figs. 33–34): $n = 14$. *Barbula vinealis* and the closely related *B. cylindrica* form one of the most perplexing complexes of mosses on the West Coast, which has been the source of numerous superfluous specific names, although possibly only several races of the same species may be involved, as pointed out several years ago (Steere 1938, 1939). Vaarama (1953b) has reported the chromosome number, $n = 13$, for *Barbula cylindrica,* from a population growing on the Stanford University Campus, so that it is certainly significant that we should have found 14 pairs very clearly in our study of many division figures in the capsules of *B. vinealis.* Cytological study of the species of *Barbula,* as already indicated, may be very helpful in furnishing further evidence bearing on their relationships. The chromosomes of *Barbula vinealis,* in several capsules studied, seem to behave very regularly during meiosis, and give no evidence of cytological irregularities that might result from recent hybridization with somewhat distantly related species, so that this species may be more distinct from *B. cylindrica* than previously believed. Our material came from two populations, from the rocky gorge of Stevens Creek, Santa Clara County (WCS 8, Feb. 12, 1953), and from San Mateo County Park, between La Honda and Pescadero (VSB 19, March 5, 1953).

Desmatodon hendersonii (Ren. & Card.) Williams (figs. 35–37): $n = 13$. This species of *Desmatodon,* a genus for which no chromosome numbers have previously been reported, has long been confused, in California and elsewhere in the West, with an eastern species, *Didymodon tophaceus* (Brid.) Jur., because of the remarkable similarity of appearance and habitat (Steere 1954). Two noteworthy cytological features are the presence of two large bivalents at the first meiotic division, as well as the constant appearance of an extremely small pair, of the order of size of accessory chromosomes (Vaarama 1949). Since the minute bivalent becomes clearly double in nature and dissociates in a perfectly normal manner, it is better considered as an unusually minute pair. Further cytological work should be most helpful in determining more accurately the relationships within the genus *Desmatodon,* which at best is an artificial one consisting of several disparate elements. Our material was collected at the foot of a small waterfall in Alum Rock State Park, near San Jose, Santa Clara County (WCS 51, April 2, 1953).

Phascum cuspidatum Hedw. var. *americanum* Ren. & Card. (figs. 38–43): $n = 26$, $n = 29$–30. Vaarama's (1953b) report of the relatively high chromosome number of $n = 52$ from a Finnish population of *Phascum cus-*

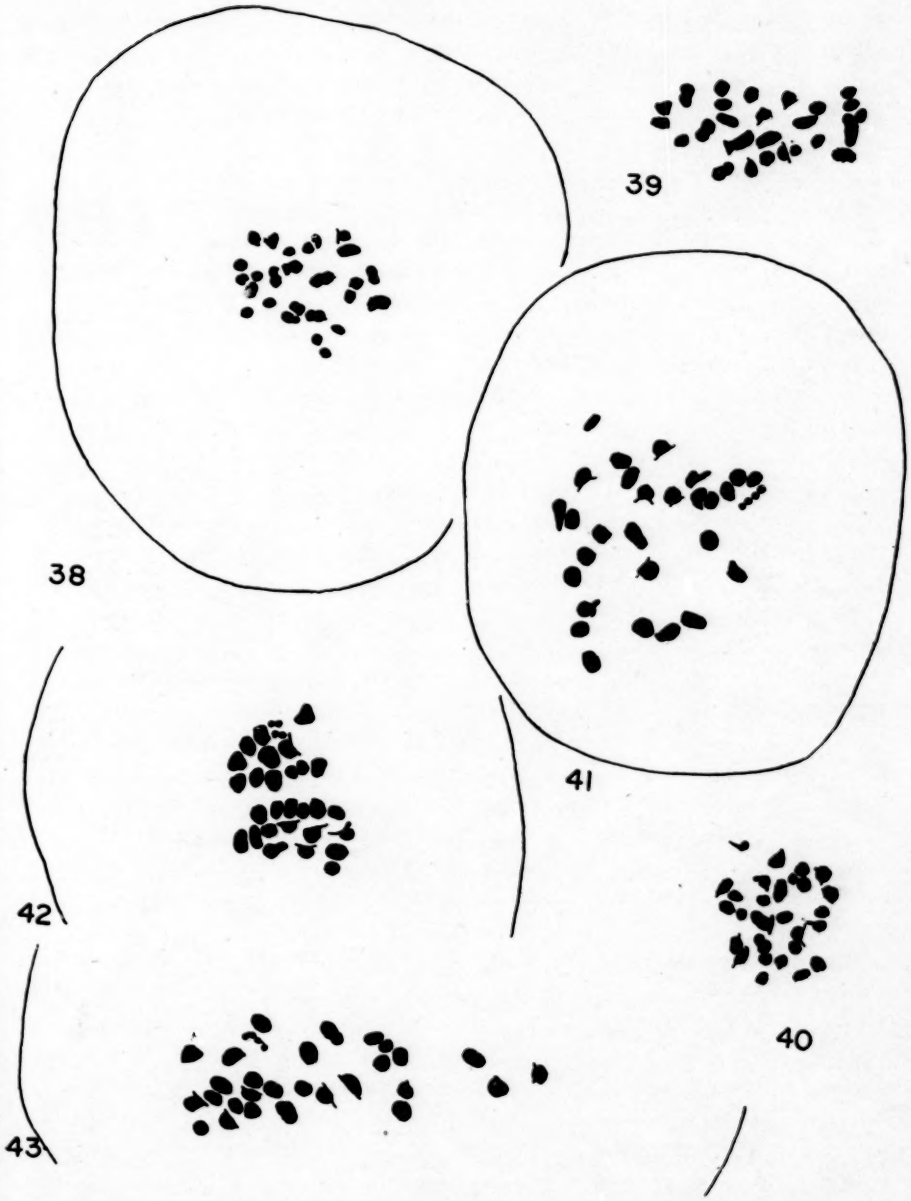

PLATE V. FIGS. 38–40. *Phascum cuspidatum* var. *americanum* (Mt. Hamilton race, $n = 26$), polar views of first meiotic metaphase. FIGS. 41–43. *Phascum cuspidatum* var. *americanum* (Sonoma County race, $n = 28 +$ "accessory chromosomes"), polar views of first meiotic metaphase. All figures $\times 2160$.

pidatum is of considerable significance in view of the obvious morphological differences between the European species and the American plants passing under the same name. Of special interest here was our discovery of two chromosome races in the California populations, which may reflect geographic isolation over a long period of time, in geological terms. Sporocytes of *Phascum cuspidatum* var. *americanum* in a population from western Sonoma County, on the west slope of the outer Coast Range, were found to have 28 pairs of normal meiotic chromosomes, plus four of the very minute chromatic bodies (figs. 41–43) that have been termed isochromosomes or accessory chromosomes by Vaarama (1949). These small chromosomes appear either as a chain of four, or as two separate pairs, and there is some question whether they should be considered as one pair that disjoins very early, or as two pairs. Another population of the same species from the north slope of Mt. Hamilton, in the Mt. Hamilton Range, shows clearly the chromosome number, $n = 26$, without any "accessory" chromosomes (figs. 38–40). Our counts of the chromosomes of these two races are based on a study of dozens of sporocytes, with the three collaborators in full agreement. It is difficult to reconcile these two chromosome complements without a study of the somatic chromosomes, which in their usually clearer morphological differences may shed some light on the relationship of what appear to be aneuploid races or populations. However, this situation probably represents the same type of aneuploidy through chromosome fragmentation that Vaarama (1953a) has described at length in *Orthotrichum tenellum*. The Sonoma County race came from a pastured hillside on the Hedgpeth Ranch (WCS 13, Feb. 22, 1953), and the Mt. Hamilton race occurs in an open area among chaparral vegetation (WCS 41, March 24, 1953). Aside from the very small chromosomes, both races show several bivalents of individual shapes, that may be recognized from figure to figure, and one very dimorphic pair may occasionally be seen, when properly oriented.

Pottia davalianum (Smith) Steere[2] (figs. 44–45): $n = 30$. Vaarama (1950b) reported the chromosome number, $n = 25$ for *P. truncata*, from Finland. The present species is quite unrelated to *P. truncata*, but there still appears to be some relationship in chromosome number, if the basic haploid number in the genus is considered to be five. As seems characteristic of the chromosomes of mosses at the first meiotic division, the bivalents are easily induced to dissociate by the application of pressure, and some counts as high as 50 were obtained from cells subjected to too much pres-

[2] *Pottia davalianum* (Smith) n. comb. *Gymnostomum davalianum* Smith, Kon. Sims Ann. Bot. 1: 577. 1805. The name, *Pottia rufescens* (Schultz) Warnst., much used by European bryologists, is a later homonym of *P. rufescens* (Hook.) C. Müll., and therefore illegitimate. *Pottia minutula* (Schleich.) Fürnr. a synonym, is also much used, but was originally described considerably later.

sure during the "squash" process. The identification of the present material is still open to some question, and we may be dealing with an undescribed species. In his monograph of the North American species of *Pottia,* Wareham (1939, p. 203) says, "*No American specimens of* Pottia *having echinate spores have been seen*" (italics his). The population reported upon here has very conspicuously spinose-papillose or echinate spores, and certainly represents some species not heretofore recognized in the United States. In view of the great variability of *Pottia davalianum* in Europe, it seems reasonably safe to assign this name to our population on a provisional basis, until further taxonomic studies can be made. Our material came from a large population on moist soil on the Stanford Campus, near Sequoia Hall (LEA 7, Feb. 19, 1953).

Timmiella vancouveriensis Broth. (figs. 46–48): $n = 14$. The chromosomes of this well-marked and very distinct genus are of unusual interest in that the bivalents are found in pairs (fig. 48) in some sporocytes, although they separate by the first metaphase. This feature is not too rare among the mosses we have studied, and would certainly seem to indicate some condition of ploidy. Furthermore, the bivalent chromosomes can often be paired up very clearly with other bivalents, by inspection, even when they are quite separate. The chromosome relationships of this genus will remain obscure until more genera of the Pottiaceae can be investigated. Our material came from a roadcut on the slopes of Mt. Tamalpais just above the Muir Woods National Monument, Marin County (WCS 58, April 8, 1953).

Tortula bolanderi (Lesq.) Howe (figs. 49–50): $n = 13$. This species, originally described from California, and still restricted to the West Coast, is an unusually clear-cut and distinctive one, easily distinguished from the other American species of *Tortula.* The chromosome number, $n = 13$, was determined with certainty at the first (fig. 49) and second (fig. 50) meiotic metaphases in a population growing at Searsville Lake, San Mateo County, southwest of the Stanford University campus (VSB 38, March 10, 1953). Another population, growing on roadside cliffs above Saratoga, Santa Clara County, near the eastern summit of the Coast Range (LEA 35, March 18, 1953) did not yield satisfactory results because of the consistent clumping of chromosomes in all sporocytes studied. The number, $n = 13$, differs somewhat from the other species in the subgenus *Syntrichia,* in which the basic number, $n = 12$, was generally observed. The chromosomal difference may well be related to the distinctiveness of this species within the genus, already mentioned.

Tortula laevipila (Brid.) Schwaegr. (figs. 51–52): $n = 12$. Although Vaarama (1953b) reported the chromosome number, $n = 15$ for this species, from a population growing on the Stanford University campus,

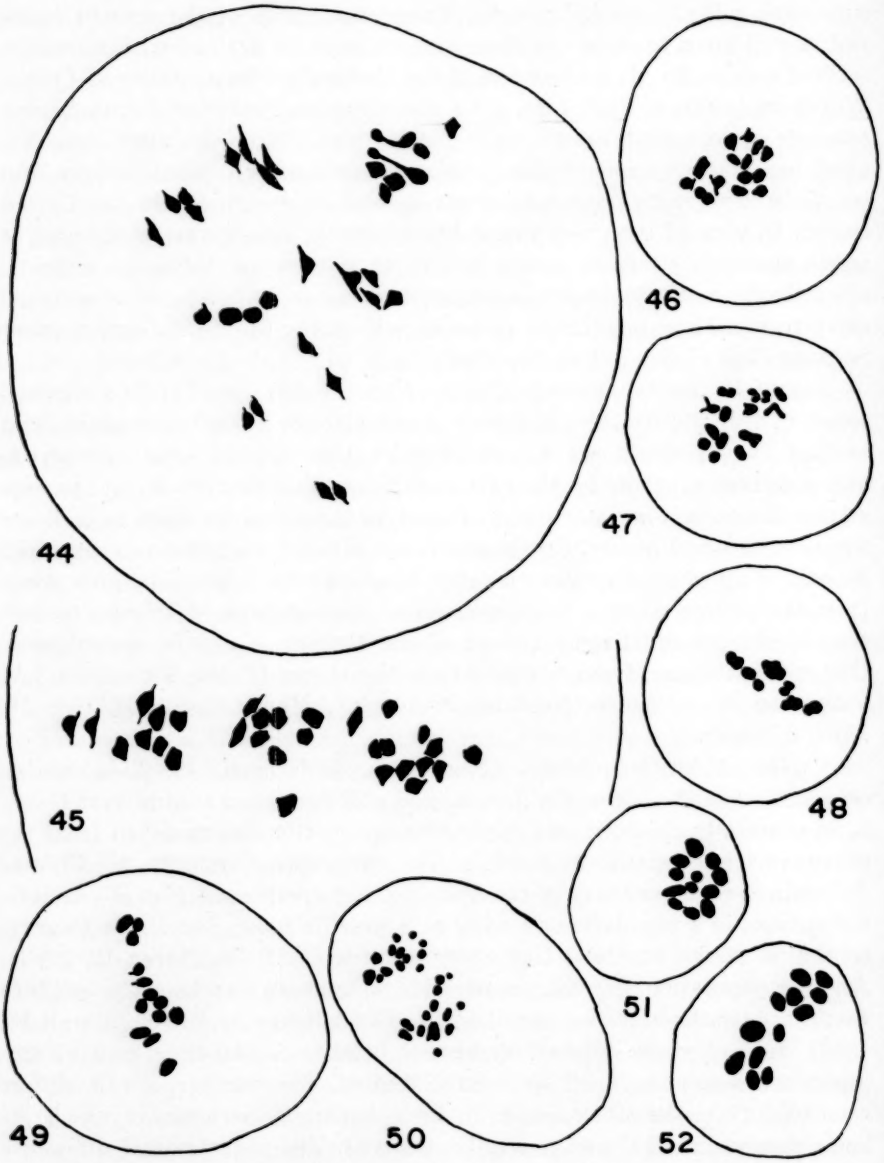

PLATE VI. FIGS. 44–45. *Pottia davalianum* ($n = 30$), first meiotic metaphase, early. FIGS. 46–48. *Timmiella vancouveriensis* ($n = 14$). FIGS. 46 and 47. First meiotic metaphase, early. FIG. 48. Multiple association of bivalents at first meiotic metaphase. FIGS. 49 and 50. *Tortula bolanderi* ($n = 13$). FIG. 49. First meiotic metaphase. FIG. 50. Second meiotic metaphase. FIGS. 51 and 52. *Tortula laevipila* ($n = 12$), polar views of first meiotic metaphase. All figures × 2160.

our material, collected on an oak near the summit of the Coast Range, on Alpine Road, in San Mateo County (VSB 47, March 31, 1953), clearly shows 12 bivalents at the first meiotic division. In view of the range of chromosome numbers reported for Californian populations of *Tortula muralis* by Vaarama (1953b), and elsewhere in this paper for *T. princeps*, we are well prepared to expect chromosome races in this clearly xerophytic species, whose chief habitat is on the bark of the California live oak, well above the ground. These races with different chromosome numbers that occur within aggregations of individuals commonly interpreted as species help to explain the variability and the taxonomic confusion of these same "species," and the reputation for being "difficult" held by the genus *Tortula*.

Tortula muralis Hedw. (figs. 53–54): $n = 48$. This species, as its name indicates, characteristically grows on masonry walls, and since it receives moisture only from rain or fog, it passes much of the year, even during the winter, in such a state of desiccation that dry plants may be rolled into dust between the fingers. When moistened, however, the plants at once regain their bright, blue-green color and continue their life processes actively, as reflected by the production of a new crop of sporophytes during any extended wet period. Nevertheless, since the maturation of the sporophyte, sporogenesis, and meiosis must certainly be affected by such drastic environmental changes, it is not surprising that chromosome races should have developed in this species. We found that the population studied, growing on a north-facing masonry wall at Memorial Court, Stanford University (WCS 5, Feb. 14, 1953), showed in its meiotic divisions a very large number of chromosomes. At the first division the smallest number seems to be 48, although in some cells as many as 51 chromosomes were counted. As the chromosomes in excess of 48 appear univalent, on the basis of size and proximity to other univalents, our final interpretation is that $n = 48$. This interpretation agrees to some extent with the findings of Vaarama (1953b), who reports that two races of *Tortula muralis* from the vicinity of Berkeley, California, have chromosome numbers of $n = 60$ and $n = 66$. These data indicate that the basic chromosome number of the species is $n = 6$, or some multiple thereof, and that, furthermore, we may expect to find many other chromosome races within this highly variable and taxonomically puzzling species.

Tortula princeps De Not. (figs. 55–61): $n = 12$, $n = 24$ (+1 accessory bivalent), $n = 36$ (+2 accessory bivalents). Three populations of this moss, the largest and handsomest species of *Tortula* in the United States, were investigated cytologically. Each population was found, by a curious coincidence, to have a different chromosome number, forming an interesting polyploid series. A population growing on the north slope of Mount Hamilton, near the summit, Santa Clara County (VSB 52, March 24, 1953) has the

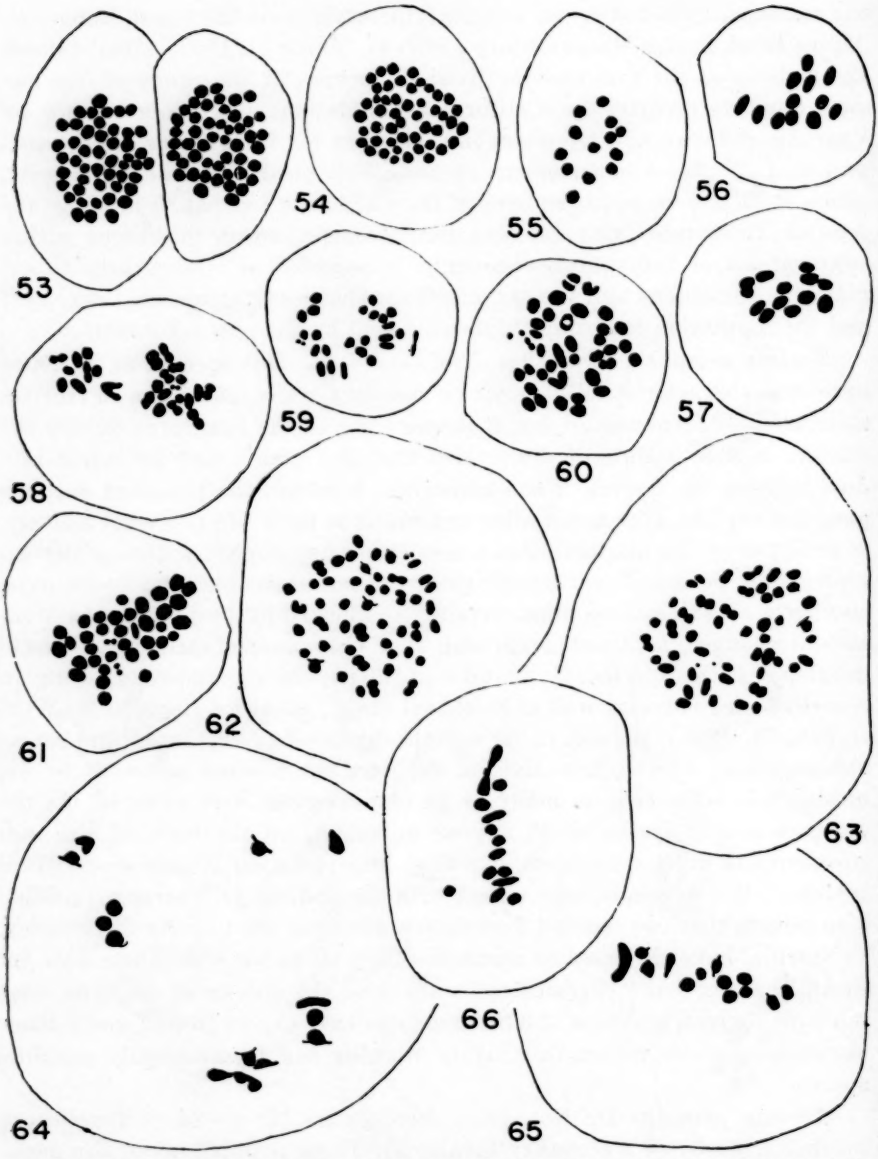

PLATE VII. FIGS. 53 and 54. *Tortula muralis* ($n = 48$), polar views of first meiotic metaphase. FIGS. 55–57. *Tortula princeps* ($n = 12$), polar views of first meiotic metaphase. FIGS. 58–59. *Tortula princeps* ($n = 24 + 1$ accessory pair), first meiotic metaphase. FIGS. 60 and 61. *Tortula princeps* ($n = 36 + 2$ accessory pairs), first meiotic metaphase. FIGS. 62 and 63. *Tortula subulata* ($n = 49$), polar views of first meiotic metaphase. FIGS. 64–66. *Weissia viridula* ($n = 13$). FIG. 64. Late diakinesis (Searsville Lake). FIGS. 65 and 66. Side view of first meiotic metaphase (Mt. Tamalpais). All figures × 2160.

chromosome number, $n = 12$, without question (figs. 55–57). No evidence appeared to support the possibility that bivalents were associated in such a way as to conceal the true chromosome number, as no quadrivalent chromosomes were seen. The chromosomes of this race behave regularly and give the impression of a well-stabilized meiotic mechanism, quite different from the situation found in the other races. Another population, from the rocky gorge of Stevens Creek, Santa Clara County, in the Coast Range (WCS 5a, February 12, 1953), proved to have 24 bivalent chromosomes of normal size and shape, plus one very tiny pair that gave evidence of precocious disjunction (figs. 58–59). The most interesting population grows at the base of oaks on the Hedgpeth Ranch in western Sonoma County (WCS 15, Feb. 22, 1953), and was found to differ greatly from the Mount Hamilton race in its irregular chromosome behavior. Many capsules and many sporocytes had to be studied before the chromosomes could be counted with any real confidence, because of the precocious dissociation of bivalent chromosomes, perhaps aided by the pressure on the cells required by the "squash" technique. The presence of numerous univalent chromosomes tended to give very high counts, but occasional early metaphase figures and the presence of two pairs of very tiny chromosomes would seem to give the keys to the chromosome number, $n = 36$ (+) (figs. 60–61). The presence of one pair of very minute chromosomes associated with 24 normal bivalents, and of two tiny pairs associated with 36 bivalents must be of some significance, in cytological behavior. No chromatic fragments or tiny chromosomes were seen in the race with 12 bivalents, but there is some possibility that such bodies could have been overlooked. The presence of three races with different chromosome numbers, in a taxonomically distinct although variable species, suggests that detailed studies of further populations from widely separated areas, as well as the investigation of somatic chromosomes, might shed valuable light on problems of speciation in mosses, as well as in other plants.

Tortula subulata Hedw. (figs. 62–63): $n = 49$. This large number of chromosomes was established without doubt in many sporocytes, although in some cells numbers as high as 52 occurred, because of the premature dissociation of bivalents. However, these disjoined homologous chromosomes could be identified not only by their proximity to each other but also by their orientation. This is one of the highest chromosome numbers reported for a natural moss population, exceeded only by *Tortula muralis* and a Finnish population of *Phascum cuspidatum* (Vaarama 1953b). It is of more than casual interest to note that these high numbers all occur in the same family. A very small single or double chromatic body was seen in most sporocytes (figs. 61–62), which seems to be a normal part of the chromosome complement. The chromosomes display unusual regularity in size,

shape, and in their meiotic behavior, indicating the relative stability of the species. Our investigation was based on a population growing on moist soil of steep banks along the highway just south of the Wawona entrance to Yosemite National Park, Mariposa County (WCS 71, April 20, 1953).

Weissia viridula Hedw. (*W. controversa* Hedw.) (figs. 64–66): $n = 13$. The chromosome number, $n = 14$, already has been reported for this variable, cosmopolitan, semi-weedy species, on the basis of material from Finland, by Vaarama (1950b). The Californian populations differ slightly in the chromosome number and also lack the conspicuous separation of chromatids in the first meiotic anaphase, reported by Vaarama, a phenomenon that may be influenced to some extent by temperature, moisture, or other external environmental conditions. The difference in chromosome number can be explained through the constant presence in the Californian populations of one chromosome pair that is conspicuously larger at the first meiotic metaphase. If this pair were to disjoin prematurely, under certain conditions, as large chromosomes may do, each half of the pair would almost certainly be taken for a bivalent chromosome, because of the comparable size. The populations studied were collected on soil on steep banks along a trail, at Searsville Lake, San Mateo County, southwest of the Stanford University campus (VSB 26, March 10, 1953), and on the middle slopes of Mt. Tamalpais, Marin County (WCS 75, April 8, 1953) (slides of the latter prepared by Grace Blanchard Iverson). The Searsville Lake population demonstrated a very considerable aberration in the spores, with relation to size and the number of nuclei. Since almost no work has been done on the percentage of sterile vs. viable spores in mosses especially as an indicator of hybridization, this observation cannot yet be properly evaluated.

Summary. The Pottiaceae, a large family of world-wide distribution, especially in dryer and more calcareous regions, consists of perhaps 80 genera and nearly 1500 species. In California, for example, this is by far the largest family of mosses, with some 20 genera and more than 60 species, comprising nearly one-fifth of the known moss flora of the state (Koch 1950, Steere 1951). In spite of the richness of species and genera, chromosome numbers have been reported previously from only five genera of Pottiaceae, from *Barbula* (3 species), *Phascum* (1 species), *Pottia* (1 species), *Tortula* (2 species) and *Weissia* (1 species). We are now able to furnish additional data for the genera just listed, in terms of further species studied, and also to add chromosome counts for members of the genera *Aloina*, *Desmatodon*, and *Timmiella*. In general, the meiotic chromosomes of this family seem to present less morphological distinctiveness and greater numbers than elsewhere among mosses, at least within our experience. Furthermore, there seems to be an exaggerated tendency for the bivalents to dissociate prematurely, and to clump, so that unusual difficulties were experi-

enced in counting chromosomes of several genera. Consequently, the need for counts of somatic chromosomes to substantiate and to correct the numbers reported from meiotic chromosomes is especially great in this family. There seems also to be a disproportionate amount of anomalous behavior of the chromosomes in the Pottiaceae for which the aneuploid races of *Phascum cuspidatum,* the polyploid races of *Tortula princeps,* and the widespread presence of accessory chromosomes may be cited as evidence. The several tendencies noted toward chromosomal irregularities may account for the fact that higher chromosome numbers occur in wild populations of the Pottiaceae than in any other family of mosses yet investigated. The only other generalization that seems possible at this time is that members of the subfamily Trichostomeae (*Barbula, Timmiella* and *Weissia*) tend to have consistently smaller chromosome numbers than members of the Pottieae (*Aloina, Desmatodon, Phascum, Pottia,* and *Tortula*). The most common basic number of chromosomes in the family appears to be 12, with a range from 11 through 14, complicated throughout by the high frequency of ploidy.

Grimmiaceae

Grimmia alpestris (Web. & Mohr) Nees (figs. 67–70): $n = 13$. This widely distributed and not uncommon species, both in Europe and in North America, does not seem to have had its chromosome number reported previously. The 13 bivalent chromosomes, as seen just before the first meiotic metaphase, fall rather clearly into several classes, in terms of their characteristic shapes (figs. 67–68). However, at the metaphase stage, as seen in polar view (figs. 69–70), the chromosomes became more similar in appearance. The chromosome behavior was very regular, unlike that in some other species of this large genus. The material studied came from a population growing on cliffs just below Wawona point, at more than 6000 feet altitude, Yosemite National Park (WCS 72, April 20, 1953). This is the only member of the section *Alpestris* to have received chromosomal study.

Grimmia apocarpa Hedw. (figs. 71–75): $n = 13$. The variability of this species is almost legendary, and the nomenclatural recognition of dozens of forms, varieties, subspecies, and species within its range of variation has resulted in a very considerable taxonomic confusion. In the most recent monograph of the species of *Grimmia* of North America, north of Mexico (Jones 1933), we find that many of the varieties ascribed to this species have themselves been given specific rank by earlier authors. The two earlier reports of the chromosome number of this species agree neither with each other, nor with the number ascertained from our investigation. Heitz (1928) reported the approximate number, n = ca. 20, whereas Vaarama (1953b) has found the chromosome number of the Finnish population investigated by him to be $n = 12$. Our material, from two widely separated populations, represent-

ing two varieties, clearly shows the chromosome number, $n = 13$. Species that are confused taxonomically may consist of several chromosomal races; although cytological studies provide data helpful in taxonomic studies, they cannot necessarily solve taxonomic problems at the specific level. The two populations studied, with the same chromosome number, differ considerably not only in the size and shape of the chromosomes, but also in such morphological features as the shape of the capsules and the leaves. Material of these two populations was sent to Dr. Geneva Sayre for identification, because of her interest in this difficult genus (cf. Sayre 1946, 1952), and we are indebted to her for the following remarks: "The two *apocarpas* do not seem to me to fall into any named varieties. If *G. apocarpa* is not a species but a spectrum, which I sometimes suspect, then No. 40 is at one end and No. 70 somewhere past the middle in the other direction. Number 40, from Mt. Hamilton, closely approaches var. *alpicola* in its broad leaves, large spores and bright red teeth. However, the capsule is oblong, not ovate, and the calyptra is mitrate. Number 70, from Yosemite, is pretty good *apocarpa*, but approaches var. *stricta* (*gracilis*), the leaves being somewhat distant and secund. Typical *stricta* has narrower leaves, a wirier stem and usually a brownish color."

Since many botanists, especially in Europe, would place this species in the segregate genus, *Schistidium*, it is interesting that it should have the same basic chromosome number as the other Californian species of *Grimmia* that were investigated. The two populations were found growing (1) on rocks along a small stream on the north slope of Mount Hamilton, Santa Clara County (VSB 40, March 24, 1953) and (2) on large boulders moistened by spray from Bridal Veil Falls, Yosemite National Park (WCS 70, April 20, 1953).

Grimmia pulvinata (Hedw.) Smith (figs. 76–77): $n = 13$. A common and variable species, the present one occurs in relatively dry and exposed places in a semi-weedy fashion. For example, it is one of the first mosses to colonize masonry walls, and exposed rocks in road cuts where it occurs in grayish cushions up to several inches across. The meiotic behavior of this species is strikingly irregular perhaps because of its xeric habitat, and its complete dependence on the occasional rains or fogs for moisture, as well as its probable hybrid ancestry. Some bivalent chromosomes obviously divide prematurely whereas others disjoin very late. As a consequence, occasional chromosomes lag behind in the cytoplasm after the formation of daughter nuclei, and sporocytes with flat metaphase plates are very difficult to find. A study of the percentage of sterility of spores in these populations would be highly desirable to determine if irregularities at meiosis result in the formation of sterile cells. Unlike flowering plants showing similar cytological anomalies, the tetrads of spores appear to be normal, and no groups of more or less

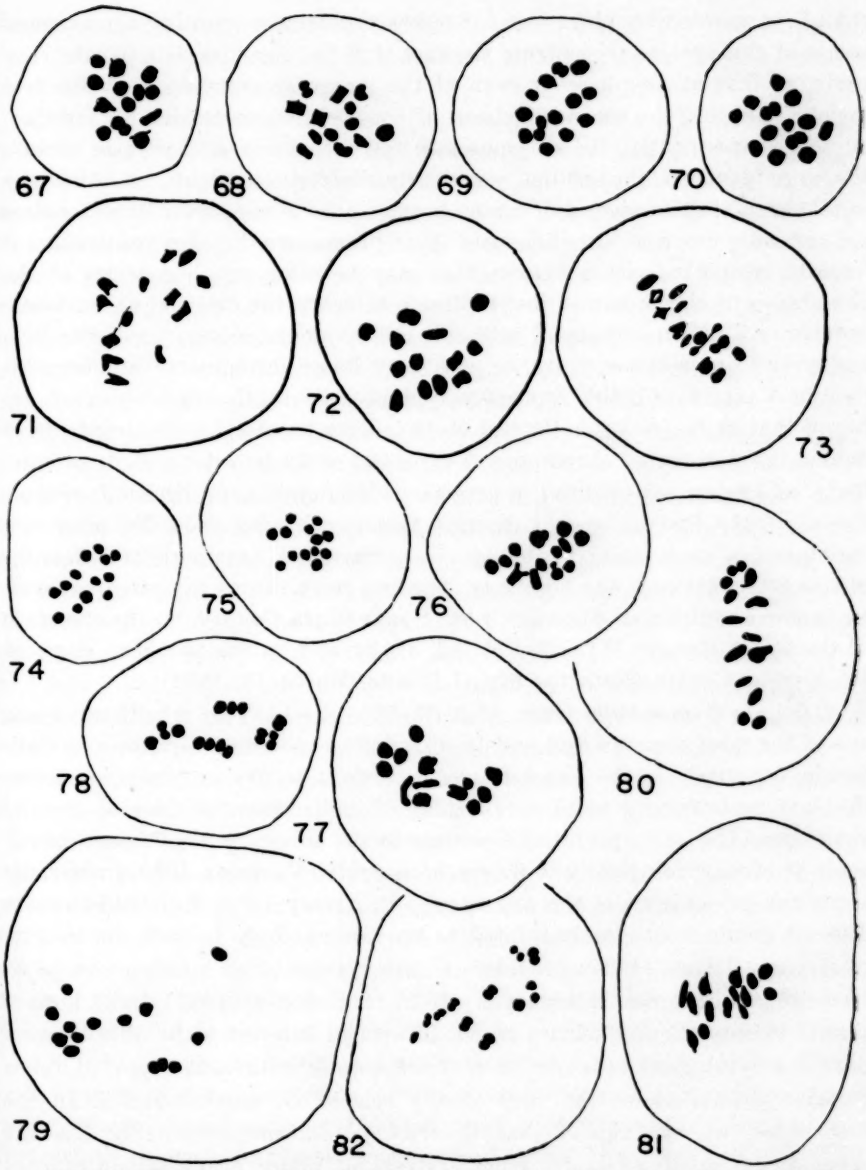

PLATE VIII. FIGS. 67–70. *Grimmia alpestris* ($n=13$). FIGS. 67 and 68. Early stage of first meiotic metaphase. FIGS. 69 and 70. Polar views of first metaphase. FIGS. 71–73. *Grimmia apocarpa* near var. *alpicola* (Mt. Hamilton, $n=13$). FIG. 71. Early stage in first meiotic metaphase. FIG. 72. Polar view of first metaphase. FIG. 73. Side view of first metaphase. FIGS. 74 and 75. *Grimmia apocarpa* near var. *stricta* (Yosemite, $n=13$). Polar views of first metaphase. FIGS. 76–77. *Grimmia pulvinata* ($n=13$). Early stages of first meiotic metaphase. FIGS. 78 and 79. *Grimmia trichophylla* ($n=13$), first meiotic metaphase. FIGS. 80–82. *Rhacomitrium depressum* ($n=14$). FIGS. 80 and 81. Side view of first meiotic metaphases. FIG. 82. Polar view of first metaphase. All figures $\times 2160$.

than four spores were observed. A further problem in counting the chromosomes of this species arises from the fact that the chromatids separate very early, so that at anaphase or even at the irregular metaphase of the first meiotic division, the second division of some chromosomes has already occurred. Consequently, the chromosomes fall into three distinct size classes, the large bivalents, the smaller, yet clearly divided univalents, and the very small chromatids or second division chromosomes. Four-parted chromosomes are not uncommon at anaphase and their premature division results in extremely complex division figures, that may be interpreted in terms of the size classes of chromosomes just outlined, to reach the original chromosome number, $n = 13$. In occasional cells, all the bivalents seemed to divide prematurely to give the appearance of a very large chromosome number. Although Vaarama (1949) reports polyploid cells in *G. muehlenbeckii,* we found that in *G. trichophylla* and *G. pulvinata* those cells seeming to have double the number of chromosomes expected could be interpreted convincingly as having experienced a precocious disjunction or division, respectively, of the first or second division meiotic chromosomes. No accessory chromosomes were found in this species, although a considerable difference in size exists between the bivalents. The two populations investigated grow on exposed boulders at Stevens Creek, Santa Clara County, on the east face of the Coast Range (WCS 9, Feb. 12, 1953) and on the southern slope of Mt. Diablo, Contra Costa County (LEA 28, March 13, 1953).

Grimmia trichophylla Grev. (figs. 78–79) : $n = 13$. This is without doubt one of the most common and widely distributed species of *Grimmia* in California, especially in the Coast Ranges, where it occurs in numerous forms that are undoubtedly more a reflection of environmental than of genetic variations. The only species of *Grimmia* in the subgenus *Eugrimmia* previously studied cytologically is *G. muehlenbeckii* (Vaarama 1949), which by a curious coincidence is the one species in a very large and traditionally difficult genus most closely related to the present one. In fact, in modern treatments, Dixon (1924) considers *G. muehlenbeckii* as a subspecies of *G. trichophylla,* whereas Mönkmeyer (1927) and Jones (1933) treat it as a simple variety. Consequently, it was of special interest to be able to compare the cytological behavior of *G. trichophylla* with that reported for a Finnish population of the very closely related *G. muehlenbeckii.* In the first place, we can report that *G. trichophylla* unquestionably has the chromosome number, $n = 13$, from a study of many preparations of capsules of a population growing on the south slope of Mt. Diablo, Contra Costa County (VSB 29, March 13, 1953), whereas Vaarama reported that the chromosome number of *G. muehlenbeckii* is $n = 14 + 2$ accessory chromosomes. Furthermore, we can report that the population of *Grimmia trichophylla* studied possesses no accessory chromosomes, and that

the chromosome complement was remarkably uniform in size and shape, in contrast to the related species, *G. pulvinata,* which seems to have larger and more differentiated chromosomes.

Rhacomitrium depressum Lesq. (figs. 80–82): $n = 14$. This chromosome number seems to have especial significance as it relates very well to the number, $n = 28$, reported by Vaarama (1949) for *R. heterostichum, R. hypnoides,* and *R. ramulosum.* Unfortunately for our purposes, however, the chromosome number of the most closely related species, *R. aciculare* Brid., has not yet been reported. *Rhacomitrium depressum* is restricted in its geographic distribution to the Pacific Coast, where it has been collected only rarely. Our material came from a population growing on wet cliffs at the entrance to Yosemite National Park, above the Merced River, Mariposa County, not far from the type locality (WCS 67, April 20, 1953).

Summary. Grimmiaceae is a relatively small family, consisting of about six genera adapted to xeric habitats, and most of the species grow on exposed rock or soil. The only genera of any magnitude are *Grimmia,* with more than 200 species described, and *Rhacomitrium,* with some 80 species. Although Heitz (1928) reported an approximate chromosome number for *Grimmia apocarpa,* all other chromosome numbers reported for members of this family seem to have been determined by Vaarama (1949, 1953b), whose excellent special study of this family will long remain the classic one, and by Yano (1951). The basic chromosome numbers in *Grimmia* and *Rhacomitrium* are 12, 13, or 14, or some multiple thereof, and show a remarkable constancy. Because of the long dry summers and the presence of extensive xeric areas, California is peculiarly rich in members of this family, and the genus *Grimmia,* with more than 20 species is, with the possible exception of *Tortula,* the largest genus of mosses in the state. The four species studied represent three sections of the genus, of which one (*Schistidium*) is widely recognized as a genus, yet the same chromosome number was encountered in all. The five species of *Rhacomitrium* whose chromosome numbers are reported by Vaarama appear to be, with one exception, tetraploid, in terms of the sporophyte, having 26 and 28 pairs. The exceptional species, *Rhacomitrium canescens,* is reported to have 12 pairs, and like *R. depressum* investigated by us, might be considered to represent the diploid condition. However, a study of the chromosome figures given by Vaarama, as well as those included here, show a considerable amount of duplication of bivalents at the first meiotic division, on the basis of size and shape. Thus, it is probable that those species of *Grimmia* and *Rhacomitrium* with 12, 13, and 14 chromosome pairs are already of a tetraploid nature.

Funariaceae

Funaria hygrometrica Hedw. (figs. 83–84): $n = 28$. This chromosome count is significant in that Vaarama (1953b) has reported the number, $n =$

14, from a population of this same ubiquitous species growing as a weed at Berkeley, in greenhouses of the University of California. The material from which this count was made came from a population growing in a pastured field under rather undisturbed conditions, accompanied by several ephemeral mosses, as *Pleuridium bolanderi, Phascum cuspidatum,* and *Ephemerum serratum,* at the Hedgpeth Ranch in western Sonoma County (WCS 11, February 22, 1953). The material was in excellent condition and showed no reduction in fertility and in the production of sporophytes in spite of its probable tetraploid nature. Furthermore, the meiotic divisions were found to be very regular. Vaarama (1950b) has reported the chromosome number, $n = 28$, from this species in Finland, but he did not indicate the source of his material, whether out-of-doors, or under glass. It would be of considerable interest to know if the weedy form so abundant in greenhouses, gardens, on burned soil, etc., represents a race different from the one which seems well established as a native plant in natural habitats. The only available evidence impinging on this question is favorable, and comes from the fact that the greenhouse race used by Wettstein (1923–24) in his important experiments also had the chromosome number, $n = 14$. It will be recalled that Wettstein was able to produce artificially, through apospory, polyploid races of *Funaria hygrometrica,* with chromosome numbers of $n = 28$ and $n = 56$, from a population in which $n = 14$.

Funaria muhlenbergii Turn. var. *patula* BSG. (fig. 85) : $n = 28$. American material of this species has not been studied previously, and this variety apparently has not been investigated at all. However, Griesinger (1937) has reported the chromosome number, $n = 26$, for the species (as *F. mediterranea*), from European material. The very great taxonomic and nomenclatural confusion over this species, and its intrinsic variability, may possibly stem from the existence of races with different chromosome numbers. A careful cytological study of these races might supply data helpful in clarifying the systematics of the species. Aneuploid races have been reported to occur in *Phascum cuspidatum,* earlier in this paper. We studied many sporocytes of this variety and can report the number, $n = 28$, with confidence. The chromosomes are remarkably uniform, not only in shape and size, but also in their behavior during meiosis. The population investigated occurs on calcareous soil near the stream in Alum Rock State Park, near San Jose, Santa Clara County (VSB 50, April 2, 1953).

Summary. The Funariaceae consist of about a dozen genera, of which only *Funaria* and *Physcomitrium* are of any size. This family has become especially well known through the notable researches of Wettstein and his collaborators on the genetics and cytology of several of its members. The artificial hybridization of species within and between the genera *Funaria, Physcomitrium,* and *Physcomitrella* have shed considerable light on the

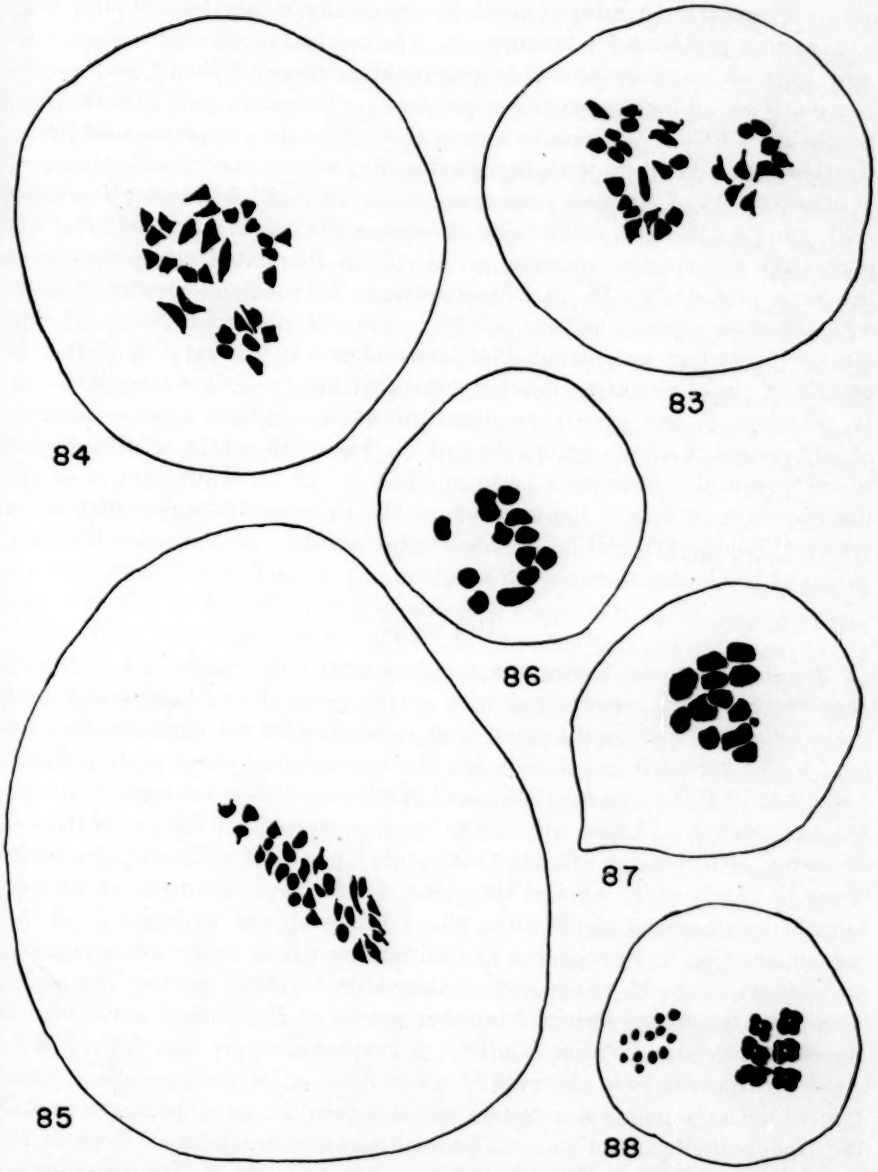

PLATE IX. FIGS. 83 and 84. *Funaria hygrometrica* ($n=28$), polar views of first meiotic metaphases. FIG. 85. *Funaria muhlenbergii* var. *patula* ($n=28$), first meiotic metaphase. FIGS. 86–88. *Bryum argenteum* var. *lanatum* ($n=12$). FIGS. 86 and 87. Polar view of first meiotic metaphases. FIG. 88. Polar view of second metaphase, multiple association of chromosomes in one plate. All figures $\times 2160$.

nature of generic boundaries in these essentially weedy mosses, and pose some serious problems for taxonomists. The production through experimentally induced apospory of highly polyploid races and hybrids in *Funaria hygrometrica* and *Physcomitrium piriforme* (Wettstein and Straub 1942, Barthelmess 1938, 1941), ranks among the outstanding experimental investigations yet carried on with bryophytes. Reports of chromosome numbers in other species of *Funaria* have been n = ca. 10 in *F. flavicans* (Beardsley 1931), and $n = 24$ in *F. californica* (Vaarama 1953b). Wettstein (1924) reported the chromosome number, n = ca. 16, in *Physcomitrella patens,* and the basic number, $n = 18$, in *Physcomitrium,* in which he produced races with the chromosome numbers, $n = 36$ and $n = 72$, under experimental conditions (Wettstein and Straub 1942, Barthelmess 1938, 1941). With the exception of the chromosome number estimated for *Funaria flavicans,* n = ca. 10, which may well need correction, the basic numbers seem reasonably closely related in all the genera studied, $n = 14$, $n = 16$, $n = 18$, with multiples which would also indicate a basic number, $n = 12$. A careful study of the somatic chromosomes of the members of the Funariaceae may well furnish evidence for the original basic chromosome number, and indicate the derivation of the higher aneuploidic numbers.

Bryaceae

Bryum argenteum Hedw. var. *lanatum* BSG. (figs. 86–88) : $n = 12$. This chromosome count, determined with certainty at the metaphases of both first and second meiotic divisions, is at variance with the chromosome number, $n = 10$ reported previously for the species from European material (Marchal 1920, Jachimsky 1935), and furthermore does not agree with the basic number, $n = 10$, that appears to be characteristic of the genus *Bryum.* However, it is not remarkable that weedy species of this sort, known to occur in nearly every part of the globe, should have aneuploid races, perhaps of geographical significance. The relationships of populations of this species growing in Europe and in California must be extremely remote, in a historical sense—if we are even dealing with the same species. The association of chromosomes observed in other species of *Bryum* was noted here at the second meiotic division (fig. 88). A further anomaly was furnished by a small chromatic body observed in a few SMC at the first meiotic division (fig. 87). The population investigated came from an open, pastured area at the Hedgpeth Ranch in western Sonoma County, on the west slope of the Coast Range (WCS 4, Feb. 22, 1953).

Bryum capillare Hedw. (figs. 89–91) : $n = 10$ (+ 2–3 accessory chromosomes). The chromosome number, $n = 10$, has already been reported for this species (Marchal and Marchal 1911, Heitz 1928), but the presence of accessory chromosomes does not seem to have been noted previously either in this

species or in the genus *Bryum*. The Marchals (1911) were able to produce a tetraploid race by experimental means in which the chromosome number was $n = 20$, which they called "var. *bivalens*." One of the most interesting features of meiotic behavior in this species is the complete association of the bivalents into five groups (fig. 90) in some sporocytes, giving some indication that this species is already diploid through duplication of the chromosome set, even though we still have not encountered any species of *Bryum* with the expected basic chromosome number, $n = 5$. The accessory chromosomes are very distinct, and likewise remain closely grouped before the first meiotic metaphase, but their behavior during the first and second meiotic divisions was not observed in detail, except that they did not seem to divide. This species is extremely widespread over the world and is also unusually variable in its morphology and its habitat preference. Consequently, several chromosome races probably exist. The population investigated grows on soil on the Stanford University Campus, near Sequoia Hall (LEA 3, Feb. 19, 1953).

Bryum pseudotriquetrum (Hedw.) Schwaegr. (*B. bimum* Schreb.) (figs. 92–95) : $n = 11$. This species differs from the others investigated, *B. argenteum* and *B. capillare,* not only in the presence of a tiny chromosome pair, but also in the difference in size and shape among the chromosomes themselves. Two much larger bivalents elongate conspicuously at early anaphase I. Although the minute chromosome was too small to show its double nature before and during the first meiotic metaphase, it was seen clearly to divide after the other chromosomes had already reached the poles (fig. 95). This species is common and abundant through all the temperate regions of the world, where it exists in many geographical races. The population investigated grows in seepage zones on roadside cliffs in Marin County, between Tomales and Petaluma (LEA 61, April 11, 1953).

Epipterygium tozeri (Grev.) Lindb. (*Pohlia tozeri* Del.) (figs. 96–99) : $n = 11$. This is the first report of a chromosome number in the small genus *Epipterygium,* which has been maintained within the generic concept of *Pohlia* by Andrews (1935). The chromosome number, $n = 11$, does not agree with the basic number, $n = 5$, characteristic of the genus *Bryum,* nor with the single chromosome count reported for the genus *Pohlia,* since in *Pohlia nutans* (Hedw.) Lindb., $n = 14$ (Heitz 1928). The bivalent chromosomes of *Epipterygium tozeri* fall very clearly into three classes, with four large ones, four of medium size, and three small ones. One of the most conspicuous features of the first meiotic metaphase is the premature separation of one very small chromosome pair into two parts, which in turn sometimes appear to be double. Furthermore, one bivalent is very definitely and strongly dimorphic when seen from the side. The material studied came from a steep shaded bank along Foothill Road, on the Stan-

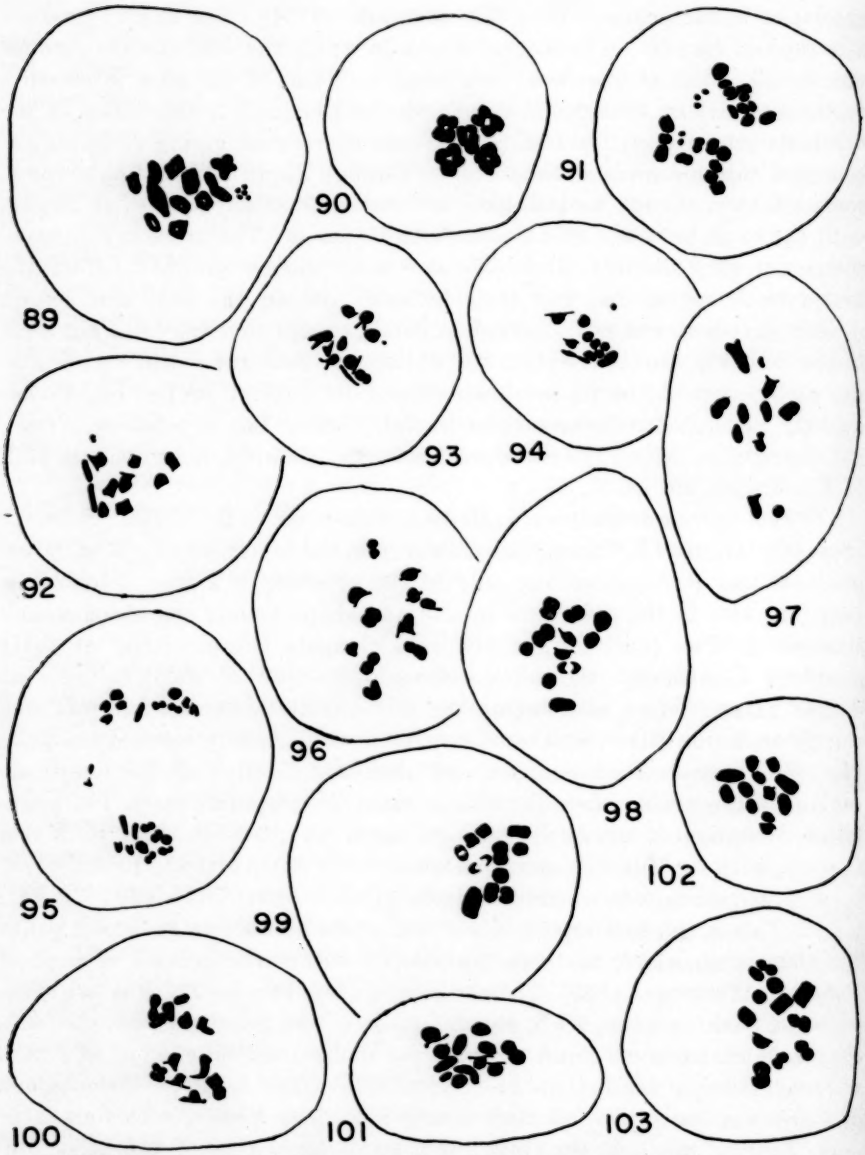

PLATE X. FIGS. 89–91. *Bryum capillare* ($n = 10 + 5$ accessory chromosomes). FIG. 89. Late diakinesis-early metaphase stage, with group of five accessory chromosomes. FIG. 90. Multiple association of chromosomes at the first meiotic metaphase. FIG. 91. First anaphase, showing apparent random distribution of accessory chromosomes. FIGS. 92–95. *Bryum pseudotriquetrum* ($n = 11$). FIGS. 92–94. Late diakinesis-early metaphase stages, showing small pair. FIG. 95. Late stage of first anaphase, showing dissociation of small pair. FIGS. 96–99. *Epipterygium tozeri* ($n = 11$), various metaphase stages, from very early to median, showing behavior of small pair. FIGS. 100–103. *Pohlia longibracteata* ($n = 12$), metaphase stages from early to median. All figures $\times 2160$.

ford Campus, Santa Clara County (WSC 17, March 4, 1953). The second population studied came from wet vertical banks, Alpine Road, near the summit of the Coast Range (WCS 48, March 31, 1953).

Orthodontium gracile Schwaegr. (figs. 104–107) : $n = 12$. In its chromosome complement of ten large bivalents, this species agrees very well with the situation characteristic of the genus *Bryum*. However, the normal bivalents are much larger than those seen in any species of *Bryum,* and are accompanied by two very much smaller pairs, of the order of size of accessory chromosomes. However, as the minute chromosomes are obviously double, and divide at the first meiotic metaphase, they are perhaps better considered as minute bivalents. The anaphase of the first meiotic division is remarkable for the complete division of the chromosomes into their chromatids, although they remain in proximity, in the same manner as reported for *Weissia viridula* by Vaarama (1950b). This seems to be the first chromosome count reported from a small genus that has been recently revised by Meijer (1951). The material investigated grew on an old, burned redwood stump in a deep forest on the east side of the Coast Range, along the La Honda Crossing Road, San Mateo County (LEA 22, March 7, 1953).

Pohlia longibracteata Broth. (figs. 100–103) : $n = 12$. Like the chromosome number of *Epipterygium tozeri,* this count does not agree either with the basic chromosome number, $n = 5$ (or $n = 10$), of the genus *Bryum,* nor with the chromosome count, $n = 14$, reported for *Pohlia nutans,* apparently the only species of the genus previously studied cytologically (Heitz 1928). *Pohlia* is a large and complex genus, taxonomically speaking, although the present species is a clear cut one, with its known geographic distribution restricted to California, Oregon and Washington. The chromosomes fall into several classes, in terms of shape and size. The specimens studied came from the San Mateo County Park, on the west slope of the Coast Range between La Honda and Pescadero (VSB 18, March 5, 1953).

Summary. Although the Bryaceae, with fewer than twenty genera, may appear small in comparison with families with more genera, such an appearance is deceptive because of the large size of several of the component genera. Nearly a thousand species have been proposed within the genus *Bryum,* alone, for example. Members of this family are found in all parts of the world, and because of the wide geographic distribution and the somewhat weedy nature of many of its species, the genus *Bryum,* especially, has been selected for considerable experimental study during the past half century. The original experiments on the development of gametophytic tissues through the regeneration of the setae of moss sporophytes (Pringsheim 1878) and the subsequent utilization of apospory in the production of polyploid races were based in part on several species of *Bryum* (Marchals 1911,

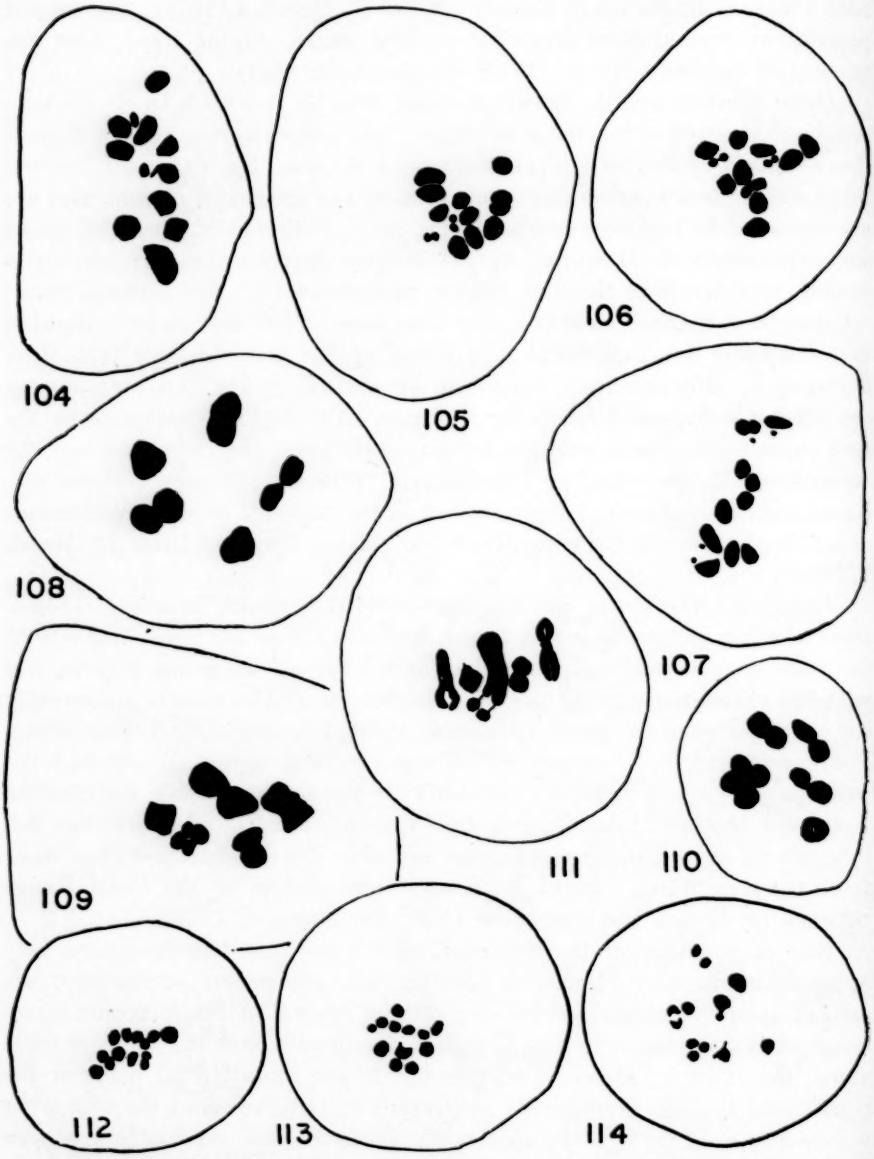

PLATE XI. FIGS. 104–107. *Orthodontium gracile* ($n = 12$), various stages of first meiotic metaphase to show behavior of two minute pairs. FIGS. 108–111. *Leucolepis menziesii* ($n = 5$). FIGS. 108–110. Polar view of first meiotic metaphase. FIG. 111. Side view of first metaphase, showing heteromorphic bivalent with satellites. FIGS. 112–114. *Aulacomnium androgynum* ($n = 12$), polar view of first meiotic metaphases. All figures $\times 2160$.

Wettstein 1924, Griesinger 1937). The present investigation tends to make the chromosomal situation in *Bryum* more complicated than realized earlier. Previous workers, almost all investigating European populations, report the chromosome number of *Bryum argenteum* as $n = 10$ (Marchal 1920, Jachimsky 1935), whereas we find twelve pairs; of *B. caespiticium* as $n = 10$ (Marchals, 1911, Wettstein 1924); of *B. capillare* as $n = 10$ (Marchals 1911, Heitz 1928), whereas we find 2–3 additional accessory chromosomes, not previously detected; and of *B. pseudotriquetrum* as $n =$ "9–10" (Heitz 1928), whereas we find an additional small bivalent, giving the count, $n = 11$. Of course, it must be realized that in species as widely distributed as those of *Bryum,* in their present interpretation at least, the presence of chromosome races may be correlated with geographical races. The only species of *Pohlia, P. nutans,* that has previously had a chromosome count reported, $n = 14$ (Heitz 1928) is only distantly related to the Californian *P. longibracteata,* so that it is not surprising for the latter to have a different basic chromosome number, $n = 12$. Two species of *Rhodobryum, R. giganteum* and *R. roseum,* have been reported to possess the chromosome number, $n = 11$ (Yano 1952). The genera, *Orthodontium* and *Epipterygium,* for which chromosome counts have not previously been reported, show basic numbers of $n = 11$ for *E. tozeri* and $n = 12$ for *O. gracile.* In summary, then, it can be seen that the basic chromosome numbers reported for members of the Bryaceae, $n = 10$, $n = 11$, $n = 12$, and $n = 14$, are reasonably consistent.

Mniaceae

Leucolepis menziesii (Hook.) Steere (figs. 108–111): $n = 5$. Lowry (1948) has reported the chromosome number, $n = 5$, for this species in his outstanding study of the somatic chromosomes of *Mnium,* from a collection made near Seattle, Washington. Lowry indicates a very considerable range of variation in the length of the somatic chromosomes, from 4.6 μ to 7.4 μ, and the meiotic chromosomes show one very large bivalent whose members tend to dissociate prematurely (figs. 108 and 109). This large chromosome may be dimorphic, although too few division figures of the proper stage were available to prove this beyond all doubt. However, since the plants are clearly dioecious, the presence of such a dimorphic pair ("sex chromosome") is highly probable. Unfortunately for any clear correlation between the somatic chromosomes of the gametophyte and the meiotic chromosomes, Lowry does not specify whether he investigated male or female plants of this species, or both. However, except for the large chromosome pair just described, the meiotic chromosomes seem to fall into the size classes established by Lowry, and no accessory chromosomes were seen. This is the only species of the present investigation in which satellites were seen in meiotic chromosomes (fig. 111). On the basis of its distinctive external morphology

alone, this species was segregated into a monotypic genus by Lindberg (1868), although retained in *Mnium* by Andrews (1940) and by Lowry (1948). However, since the chromosome morphology differs so markedly from that of any known species in *Mnium*, and a different basic number occurs, there seems to be abundant reason for recognizing the genus *Leucolepis* as valid. The population investigated occurs on the wet, rocky bank of a stream, under redwoods, in San Mateo County Park, between La Honda and Pescadero (LEA 21, March 5, 1953).

Summary. The Mniaceae is a relatively small family, consisting of very few genera, but the individual plants of many species are conspicuously large and handsome. Perhaps for this reason, more species in *Mnium* have been studied cytologically than in any other genus of mosses, even in much larger ones. The extensive cytotaxonomic study of *Mnium* by Lowry (1948) has been supplemented by the more recent work of Vaarama (1950b) and Tatuno (1951). The basic chromosome numbers in *Mnium*, in over 20 species studied, are $n = 6$ and $n = 7$, or, in a few species multiples thereof. Although *Mnium microphyllum* and *M. flagellare*, which have been segregated into the genus *Trachycystis* (Lindberg 1868) on the basis of morphological structure, the chromosome number, $n = 7$, reported for both species by Tatuno (1951) gives little cytological support for such a generic separation. With respect to other genera, Lowry (1948) reported the chromosome number, $n = 14$, for a single species of *Cinclidium, C. stygium*, and the number, $n = 5$, for *Leucolepis menziesii* (as *Mnium*), as already noted under that genus.

Aulacomniaceae

Aulacomnium androgynum Schwaegr. (figs. 112–114): $n = 12$. The chromosome number of this species was estimated as $n = 10$–11 by Heitz (1945). The study of many sporocytes of a Californian population resulted consistently in the determination of the chromosome number as $n = 12$, a discovery of considerable interest, since it agrees with the report by Vaarama (1950), of $n = 12$ for *A. palustre*, whose chromosome number had been estimated as $n =$ "(9)10" by Heitz (1928). The chromosomes differ considerably in size, with two very large bivalents (fig. 114), several very small ones, and at least one pair that is distinctly dimorphic in side view. This species is very common on rotting wood in the coniferous forests of California, both in the Coast Ranges and in the Sierra. The material investigated here grew on a rotting redwood log in the Big Basin State Park, Santa Cruz County (VSB 42, March 18, 1953).

Summary. The Aulacomniaceae consists of two widely distributed genera, *Aulacomnium* and *Leptotheca*, and the small total of approximately a dozen species. Nevertheless, we find published references to the chromosome numbers of two species of *Aulacomnium*, estimated for *A. andro-*

gynum and *A. palustre* by Heitz (1928, 1945), and a definite report for the latter species by Vaarama (1950b). Both species appear to have the same chromosome number, $n = 12$.

Bartramiaceae

Anacolia menziesii (Turn.) Paris (figs. 115–118) : $n = 8$. In sharp contrast to its variety *baueri,* which will be treated next, this species shows more regular cytological behavior, although occasional late anaphases show some variation in the rate of chromosome movement. The division figures studied showed very clearly the presence of seven large bivalent chromosomes, and a very small pair that dissociates precociously. The basic chromosome number, $n = 8$, agrees well with that reported for other members of the family, especially for *Bartramia.* This is the first member of the genus *Anacolia* to have its chromosome number counted. The material studied was collected near the summit of the Coast Range, above Saratoga, Santa Clara County (WCS 34, March 18, 1953).

Anacolia menziesii (Turn.) Paris var. *baueri* (Hampe) Paris (figs. 119–121) : $n = 7$. From the irregular behavior of the chromosomes at meiosis, especially in terms of precocious and laggard disjunction of chromosomes at the first meiotic division (figs. 120 and 121), there must be some genetic imbalance, perhaps due to hybridization. In addition to the presence of univalent chromosomes at a time when they would ordinarily not be encountered, accurate counts are made still more difficult by the premature division of anaphase chromosomes. Although originally proposed as an independent species, this moss is now considered to be only a variety of *A. menziesii,* from which it differs in the cylindrical or oblong, rather than spherical capsule, the longer seta, and the smaller spores which are ornamented differently. Furthermore, the variety seems to prefer distinctly drier habitats. It is perhaps significant that a marked chromosome difference should be correlated with morphological and ecological differences. The taxonomic problems in *Anacolia* have recently been reviewed thoroughly by Flowers (1952). The population studied here came from a steep shaded roadside bank on the south slope of Mt. Diablo, Contra Costa County (VSB 27, March 13, 1953).

Summary. The Bartramiaceae, although consisting of only about ten genera, is a relatively large family, since *Bartramia* and *Breutelia* each contain over 100 species, and *Philonotis* nearly 200 species. Furthermore, the family is represented in all parts of the world, from the coldest to the warmest climates, in all latitudes. In general, although some of the species tolerate very exposed situations, most of them seem to have a rather high water requirement. Previously reported chromosome counts in the Bartramiaceae are $n = 8$ for *Bartramia pomiformis,* from a Japanese popula-

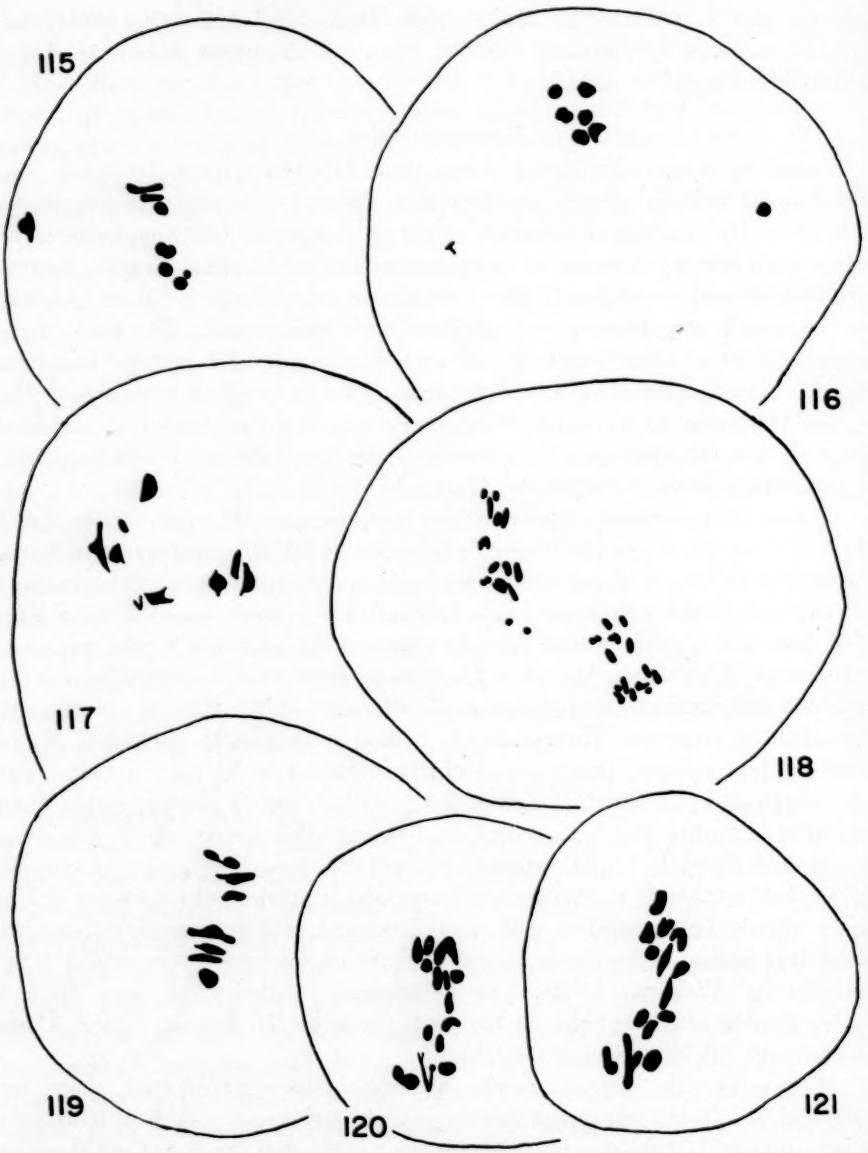

PLATE XII. FIGS. 115–118. *Anacolia menziesii* ($n = 8$). FIGS. 115–117. Very early stages of first meiotic metaphase. FIG. 118. Late anaphase of first division showing precocious dissociation. FIGS. 119–121. *Anacolia menziesii* var. *baueri* ($n = 7$) FIG. 119. Side view of first meiotic metaphase. FIGS. 120 and 121. Anaphase stages of first division. All figures × 2160.

tion (Kurita 1937) and for its var. *crispa,* in Finland (Vaarama 1950b); and $n = 12$ for *B. ithyphylla,* from Finland (Vaarama 1950b). For *Philonotis fontana,* Heitz (1928) estimated a chromosome number, $n = 7–8$, whereas Vaarama (1953b) definitely reports the number, $n = 6$, from a population in southern Finland. No American material of this family has been previously studied cytologically.

Hedwigiaceae

Hedwigia ciliata (Hedw.) Brid. (figs. 122–124): $n = 11$. The chromosome number we have established for a Californian population is of special interest in that it is just half the chromosome number, $n = 22$, reported by Vaarama from Finnish material (1950b). A small chromosome that disjoins prematurely presents another feature of interest in our material. This species has, for mosses, an astonishingly wide geographical distribution, occurring in every continent, including Australia, and even extending throughout the tropics at higher altitudes. In view of its morphological variability and wide distribution, the presence of chromosome races is perhaps to be expected. Our material occurred on a large, exposed boulder along a stream on the west face of Mount Hamilton, Santa Clara County (LEA 46, March 24, 1953).

Pseudobraunia californica (Sull.) Broth. (*Braunia californica* Sull.) (figs. 125–126): $n = 11$. This is the first report of a chromosome number from a monotypic genus restricted in its geographic distribution to the Pacific Coast of North America, from California to British Columbia. Some significance should certainly be placed on the fact that the chromosome number agrees with that of Californian material of the related genus *Hedwigia,* in the same small family. The chromosomes at the first meiotic anaphase are remarkable for the distinct separation of the chromatids (fig. 126), as reported by Vaarama (1950b) for *Weissia viridula,* so much so that if it were not for their proximity, they might greatly confuse the counting of chromosomes. The chromosomes fall into several clear-cut classes on the basis of their size and shape. The population investigated was collected on a boulder at the Hedgpeth Ranch in western Sonoma County (WCS 20, Feb. 22, 1953).

Summary. Consisting of a half-dozen small genera, the Hedwigiaceae seem to reflect very ancient origins, in terms of the geographical distribution and specialized morphology of most members. Only one representative of the family, the single species of the genus *Hedwigia,* has been studied cytologically. Vaarama (1950b) found the chromosome number, $n = 22$, in a Finnish population, whereas in the Californian material, $n = 11$. The genus *Pseudobraunia,* also with a single species, *P. californica,* was found to have the chromosome number, $n = 11$. The agreement of the two genera

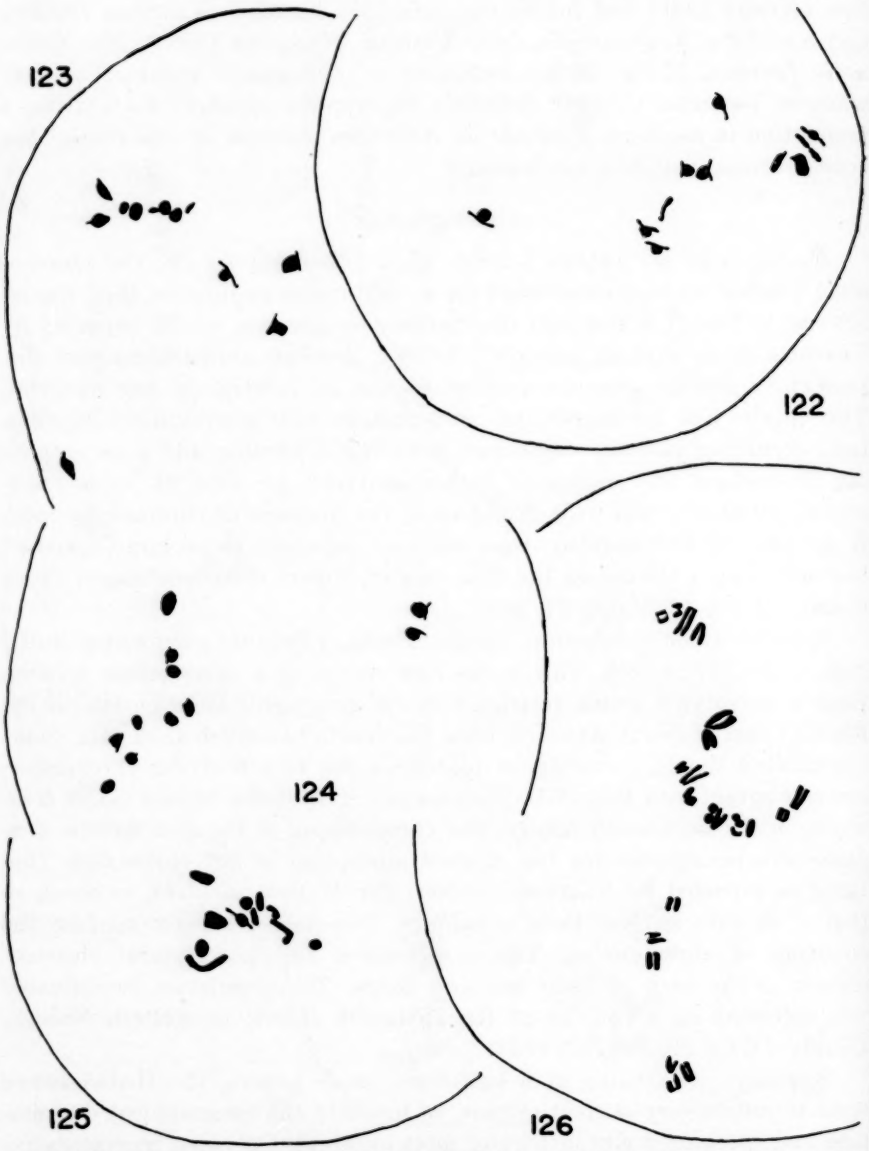

PLATE XIII. FIGS. 122–124. *Hedwigia ciliata* ($n = 11$), various stages of first meiotic metaphase, from early to median. FIGS. 125 and 126. *Pseudobraunia californica* ($n = 11$). FIG. 125. First meiotic metaphase, early. FIG. 126. First anaphase, late, showing premature division of univalent chromosomes. All figures $\times 2160$.

in their chromosome number may certainly be taken to some degree as positive evidence of their relationship.

ORTHOTRICHACEAE[3]

Orthotrichum affine Brid. (figs. 127–129): $n = 6$. The chromosomes of this species seemed to be unusually uniform in size and shape, among the group of species in which $n = 6$. The population studied occurs on moist shaded rocks and at the base of trees at Mirror Lake, Yosemite National Park, Mariposa County (WCS 64, April 20, 1953).

Orthotrichum bolanderi Sull. (figs. 130–133): $n = 6$. This well-marked species is endemic to California and is not uncommon in the San Francisco Bay area. The chromosome number, $n = 6$, seems very certain in both meiotic divisions, since it was established in large numbers of sporocytes from two populations. The only unusual behavior observed was the appearance in a single sporocyte of very small chromatin bodies in two of the four anaphase chromosome groups, in the second meiotic division (fig. 133). Material from both populations studied occurred on vertical rock faces, one from a rocky knob near Searsville Lake, San Mateo County, a few miles west of Stanford University (LEA 23, March 10, 1953), and from near the summit of Mt. Diablo, Contra Costa County (LEA 24, March 13, 1953).

Orthotrichum cylindrocarpum Lesq. (figs. 160–163): $n = 11$. This species is closely related to *O. tenellum* and considered as a variety of it by Koch (1950), but is maintained as a separate species by Grout (1946) in the most recent monographic treatment of the North American members of the family.

The chromosome behavior of the two forms at meiosis seemed very similar, in that both possess ten normal bivalents and one very small pair. The only difference noted was that the minute bivalent apparently lags in its disjunction, instead of dissociating precociously, since it showed no signs of doubleness at the first metaphase. The material was collected on the trunk of a roadside oak south of Olema, Marin County (WCS 74, April 28, 1953).

Orthotrichum lyellii Hook. & Tayl. (figs. 134–136): $n = 6$. The chromosomes of this species show more individuality and seem to be larger than those of the related species with six bivalent chromosomes. This species is a very common one on the West Coast from British Columbia to Mexico, and is the largest and most abundant *Orthotrichum* in California, where it forms large black tufts on trees or more rarely on rocks in regions in which fog is prevalent. Of the several populations studied, two may be

[3] Since a detailed account of the chromosome behavior and the cytotaxonomy of *Orthotrichum* is in preparation and will appear separately, the results are given here in abridged form, for the sake of completeness in the present report.

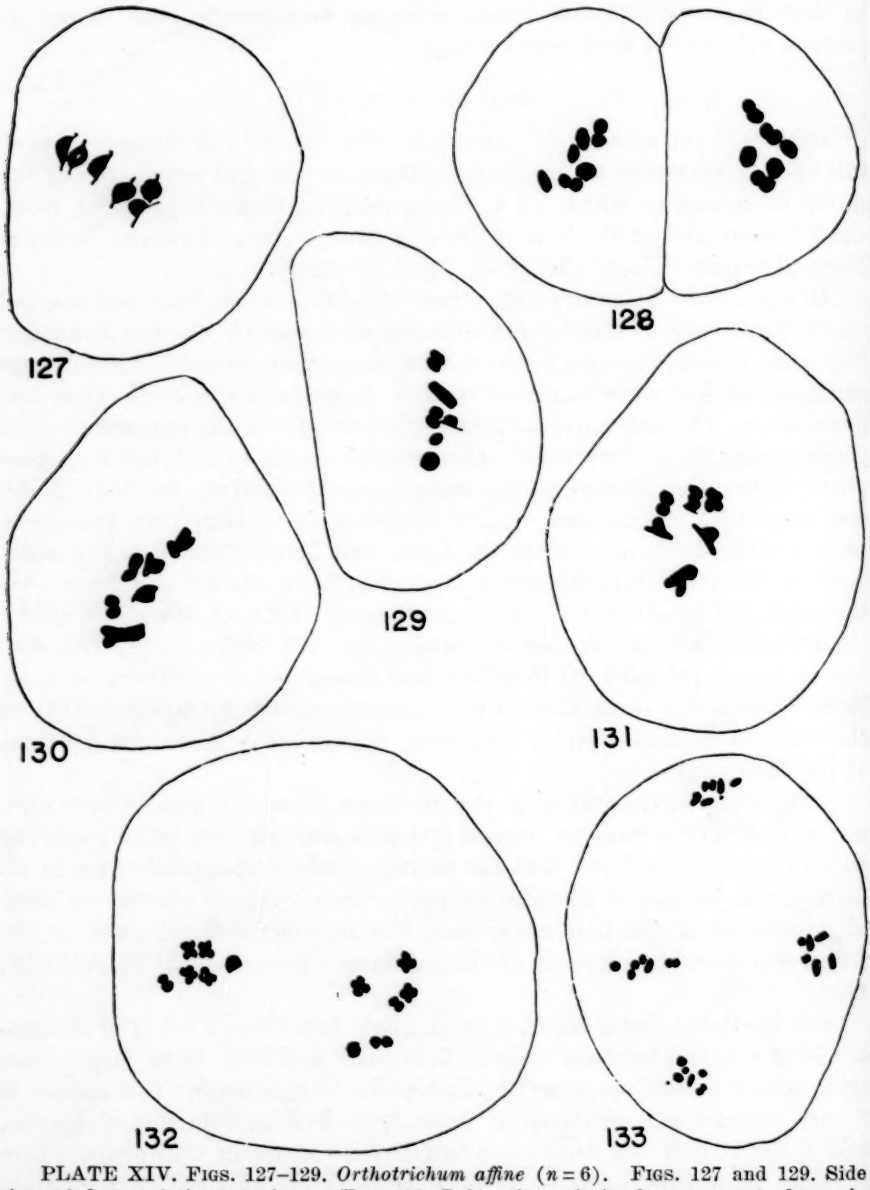

PLATE XIV. FIGS. 127–129. *Orthotrichum affine* ($n = 6$). FIGS. 127 and 129. Side view of first meiotic metaphase. FIG. 128. Polar view of simultaneous metaphases in sister sporocytes. FIGS. 130–133. *Orthotrichum bolanderi* ($n = 6$). FIGS. 130 and 131. Early stages of first meiotic metaphase. FIG. 132. Anaphase of first division, late. FIG. 133. Late anaphase stage of second division, with chromatic fragments in two nuclei. All figures $\times 2160$.

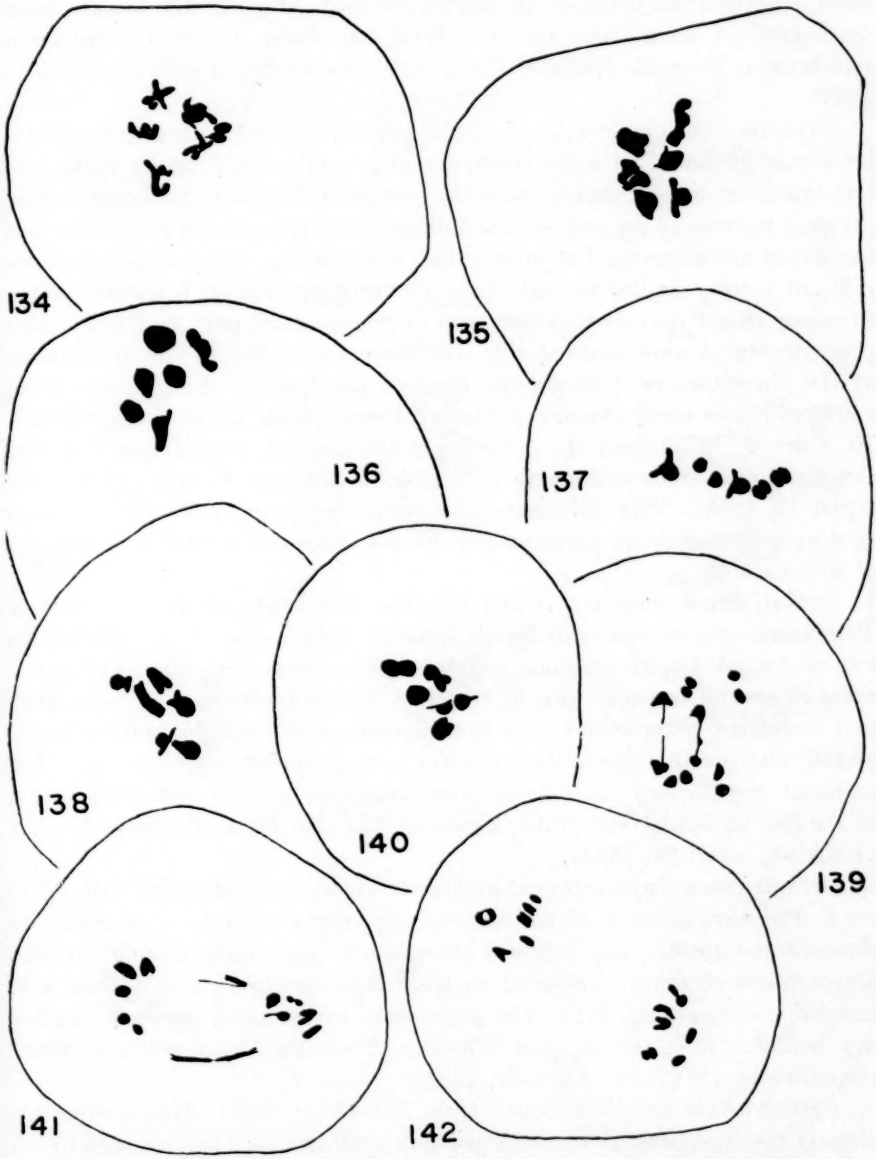

PLATE XV. FIGS. 134–136. *Orthotrichum lyellii* ($n = 6$). FIG. 134. Late diakinesis stage, showing chiasmata. FIGS. 135 and 136. Early and median metaphases, respectively, of first meiotic division. FIGS. 137–139. *Orthotrichum rupestre* ($n = 6$). FIGS. 137 and 138. Stages of first meiotic metaphase. FIG. 139. First anaphase, showing some irregularity of disjunction. FIGS. 140–142. *Orthotrichum rupestre* var. *globosum* ($n = 6$). FIG. 140. Early metaphase, first meiotic division. FIG. 141. Anaphase of first division, with some irregularity of disjunction. FIG. 142. Telophase of first division. All figures $\times 2160$.

cited, one from the trunk of an oak on the south slope of Mt. Diablo, near the summit, Contra Costa County (WCS 25, March 13, 1953), and from tree trunks, Yosemite National Park, Mariposa County (VSB 54, April 5, 1953).

Orthotrichum rivulare Turn. (figs. 146–153): $n = 11$. In a genus characteristically found in xeric environments, usually growing on rocks and tree-trunks at some distance above the ground, this species is conspicuously atypical because of its amphibious habitat along streams, on rocks and tree bases that are submerged at high water. Nevertheless, the chromosome complement is very similar to that of the distantly related *O. tenellum*, in the presence of ten normal bivalents and one very small pair that dissociates precociously. A very considerable difference was noted in the appearance of the chromosomes, however, in the two populations studied, one from boulders in the rocky canyon of Stevens Creek, Santa Clara County (LEA 10, Feb. 12, 1953), and the other from the base of trees along Robinson Creek, a few miles southwest of Ukiah, Mendocino County (WCS 66, April 11, 1953). This difference may reflect either a minor chromosomal race or only metabolic variations in plants subjected to different degrees of desiccation.

Orthotrichum rupestre Schleich. (figs. 137–139): $n = 6$. This widely distributed species occurs in North America only in the Rocky Mountains and westward. The chromosome number, $n = 6$, observed in dozens of sporocytes in several capsules, can be recorded with confidence. One very large and elongated chromosome pair is conspicuous at the first meiotic metaphase, whereas the other bivalents are approximately equal in size. The material investigated came from large boulders, usually wet with spray, at the foot of Bridal Veil Falls, Yosemite National Park, Mariposa County (LEA 68, April 20, 1953).

Orthotrichum rupestre var. *globosum* (Lesq.) Grout (figs. 140–142): $n = 6$. The chromosomes of the variety are very similar in appearance to those of the species, but behaved much more irregularly during meiosis. Many sporocytes were observed to have lagging chromatids at the first meiotic anaphase (fig. 141). The population investigated grows on rather dry boulders in a ravine near Wawona, Yosemite National Park, Mariposa County (WCS 65, April 20, 1953).

Orthotrichum tenellum Bruch (figs. 154–159): $n = 11$. This species has already received detailed cytological study by Vaarama (1953a), who found different chromosome numbers in two capsules collected from the same population on the Stanford Campus. In one capsule, according to Vaarama, the sporocytes had 9 bivalents of normal size and two very small chromatic bodies, whereas in the other capsule, the sporocytes possessed 10 normal bivalents and one very minute chromatic body. In a half dozen capsules

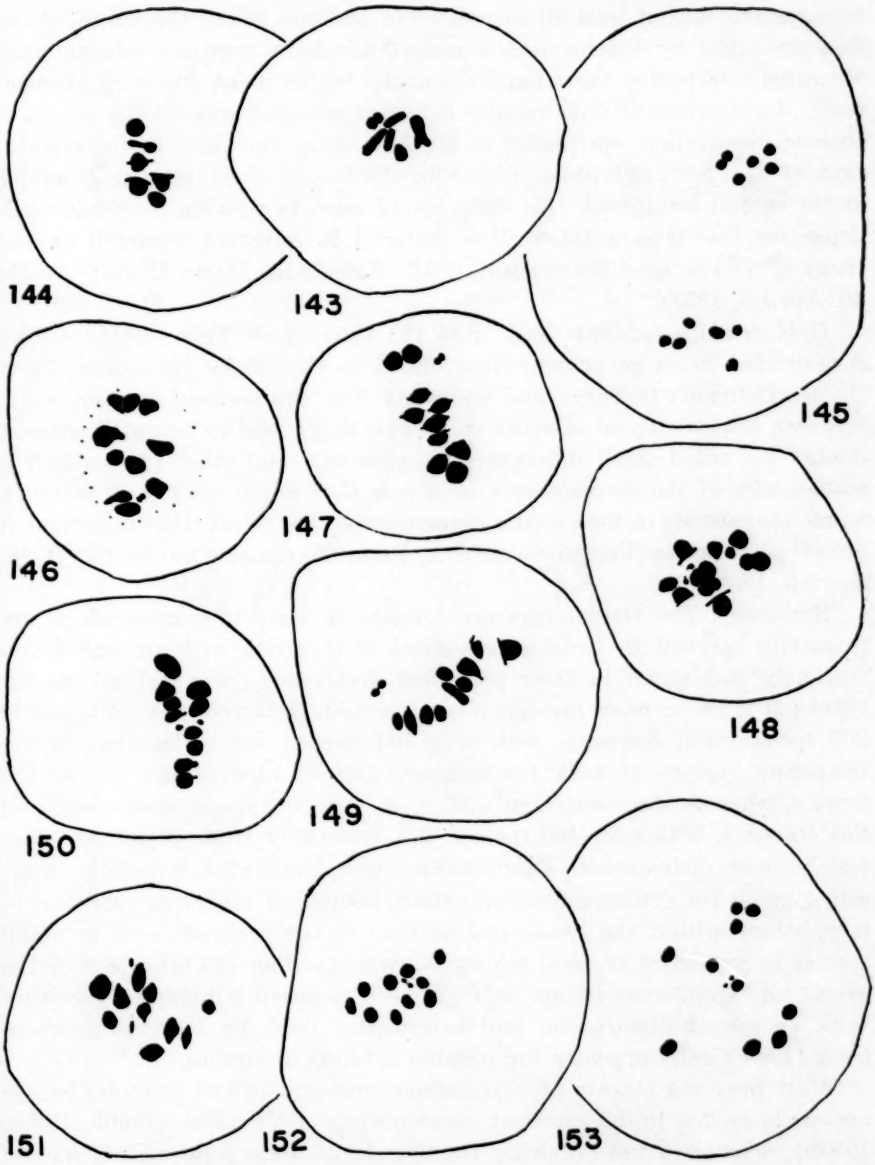

PLATE XVI. FIGS. 143–145. *Orthotrichum texanum* ($n = 6$). FIGS. 143 and 144. Early stages of first meiotic metaphase. FIG. 145. Metaphase of second division. FIGS. 146–151. *Orthotrichum rivulare* (Santa Clara County, $n = 11$). FIG. 146. Diakinesis stage, nuclear membrane still visible. FIGS. 147–151. Various stages of first meiotic metaphase, to show behavior of minute pair. FIGS. 152 and 153. *Orthotrichum rivulare* (Mendocino County, $n = 11$), polar view of first metaphases. All figures $\times 2160$.

investigated, and at least 50 sporocytes in each, we found the second situation described by Vaarama—ten normal bivalents and one minute pair. Vaarama interpreted the minute chromatic bodies to be accessory chromosomes, but because of their regular behavior, except for small size and precocious dissociation, we prefer to consider them one pair. Their orientation at the first metaphase (figs. 157–158) and their regular behavior at the second metaphase (fig. 159) would seem to provide conclusive evidence for this interpretation. The material investigated occurred on the trunk of *Thuja*, near the summit of Mt. Tamalpais, Marin County (WCS 60, April 8, 1953).

Orthotrichum texanum Sull. (figs. 143–145): $n = 6$. This western species is restricted in its geographic distribution to the Rocky Mountains, from British Columbia to Texas, and westward. The chromosome number, $n = 6$, was seen consistently in so many sporocytes that it can be accepted without doubt. We noted small differences between this and other species in the morphology of the chromosomes, of a sort that might very well be much more recognizable in the somatic chromosomes. The population investigated grows on rocks in Yosemite National Park, Mariposa County (VSB 56, April 5, 1953).

Summary. The Orthotrichaceae consists of some 15 genera which are primarily tropical in their geographical distribution and are rather remarkably specialized in their ecological preference for a habitat on the trunks of trees, or more rarely, on rocks or soil. *Orthotrichum*, with nearly 200 species, and *Zygodon*, with over 100 species, are widespread in the temperate regions of both hemispheres, and at higher altitudes in the tropics, whereas *Macromitrium*, with more than 400 species described, and *Schlotheimia*, with over 100 species, are essentially tropical and subtropical in their distribution. *Macromitrium* would make an especially interesting genus for cytological investigation, because of the great variation in morphology within the genus and because of the occurrence of so many species in any moist tropical region. Notwithstanding the large size of the genus, no chromosome counts have yet been reported, although interesting work on sexual dimorphism and heterospory done by Ernst-Schwarzenbach (1944), calls urgently for parallel cytological studies.

Most previous reports of chromosome numbers in the Orthotrichaceae appear to be due to the excellent pioneer work of Vaarama (1950b, 1953a, 1953b), who gives the following counts: *Amphidium lapponicum*, $n = 16$; *Orthotrichum speciosum*, $n = 6$; *O. stramineum*, $n = 13$; *O. tenellum*, $n = 9$–10, plus accessory chromosomes; and *Ulota curvifolia*, $n = 21$, plus accessory chromosomes. Although the present authors are reporting more fully elsewhere on chromosomal behavior in the Orthotrichaceae, it seems worthwhile to call attention to the fact that all Californian populations belong-

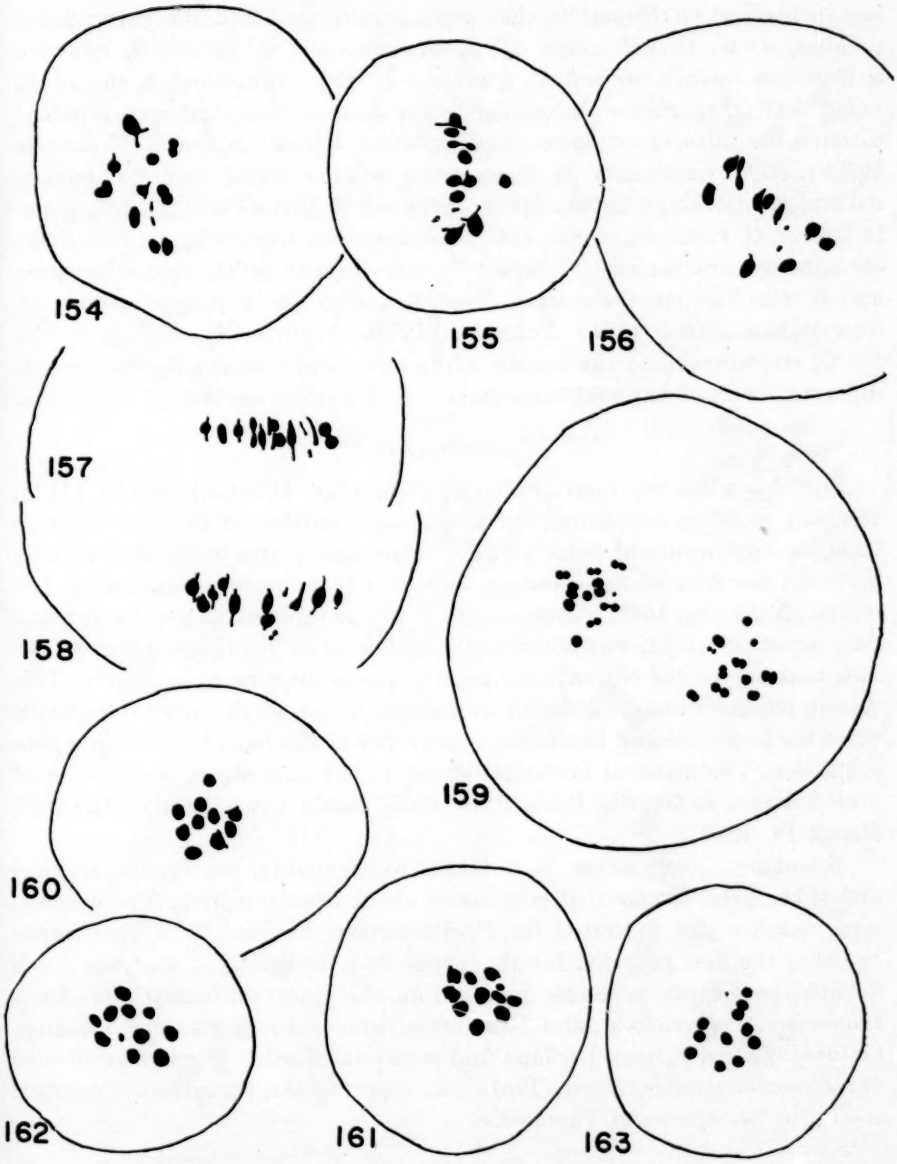

PLATE XVII. FIGS. 154–159. *Orthotrichum tenellum* ($n = 11$). FIGS. 154–158. Various stages of first meiotic metaphase, from early to median, to show behavior of minute pair that dissociates precociously. FIG. 159. Metaphase of second division in polar view. FIGS. 160–163. *Orthotrichum cylindrocarpum* ($n = 11$), polar view of first meiotic metaphases. All figures $\times 2160$.

ing to the section *Rupestria* that were investigated had the chromosome number, $n = 6$: *Orthotrichum affine, O. bolanderi, O. lyellii, O. rupestre* and its var. *globosum,* and *O. texanum.* In this connection, it should be noted that *O. speciosum,* belonging to the same section, has been reported to have the same chromosome number, from Finnish material (Vaarama 1950b). Such uniformity of chromosome number would seem to indicate natural relationships for the species grouped in this section. In two populations of *O. rivulare,* in the well-marked section *Rivularia,* we found the chromosome number, $n = 11$, which is also present in *O. cylindrocarpum* and *O. tenellum,* in the section *Tenella,* and in the Japanese species, *O. consobrinum* (Yano 1951). Vaarama (1953b) reports the number, $n = 13$, for *O. stramineum,* of the section *Straminea,* which would indicate a still different series of chromosome numbers in a further section of the genus.

Neckeraceae

Porothamnium bigelovii (Sull.) Fleisch. (figs. 164–166): $n = 12$ (11?). The only question concerning the chromosome number of this species arose from the appearance of polar views of metaphase plates of the first meiotic division; one pair of chromosomes appeared to be recently separated, but still adjacent (fig. 166). Furthermore, in pre-metaphase stages, the chromosome number, $n = 11$, was occasionally encountered, lending support to the idea that one of the chromosome pairs perhaps disjoins prematurely. This species possesses unusually small sporocytes, a fact all the more remarkable when the large size and handsome appearance of the moss is taken into consideration. The material investigated was found on a steep, rocky bank of a cold stream in the Big Basin State Park, Santa Cruz County (LEA 30, March 18, 1953).

Summary. Neckeraceae is a large, wide-ranging, essentially tropical and subtropical family that consists of about twenty genera. The chromosome number just indicated for *Porothamnium bigelovii* is of importance in being the first reported for the genus. It is to be hoped that the much debated taxonomic problems involved in the interrelationships of *Porothamnium, Porotrichum,* and *Thamnium,* which have led to much nomenclatural confusion, may perhaps find some clarification through continued chromosomal studies. Yano (1951) has reported the chromosome number, $n = 11$, in two species of *Thamnium.*

Thuidiaceae

Claopodium whippleanum (Sull.) Ren. & Card. (figs. 167–169): $n = 11$. The chromosomes of this very abundant and almost weedy Californian species fall into widely differing size classes at the first meiotic metaphase. Furthermore, the members of one small bivalent tend to disjoin prema-

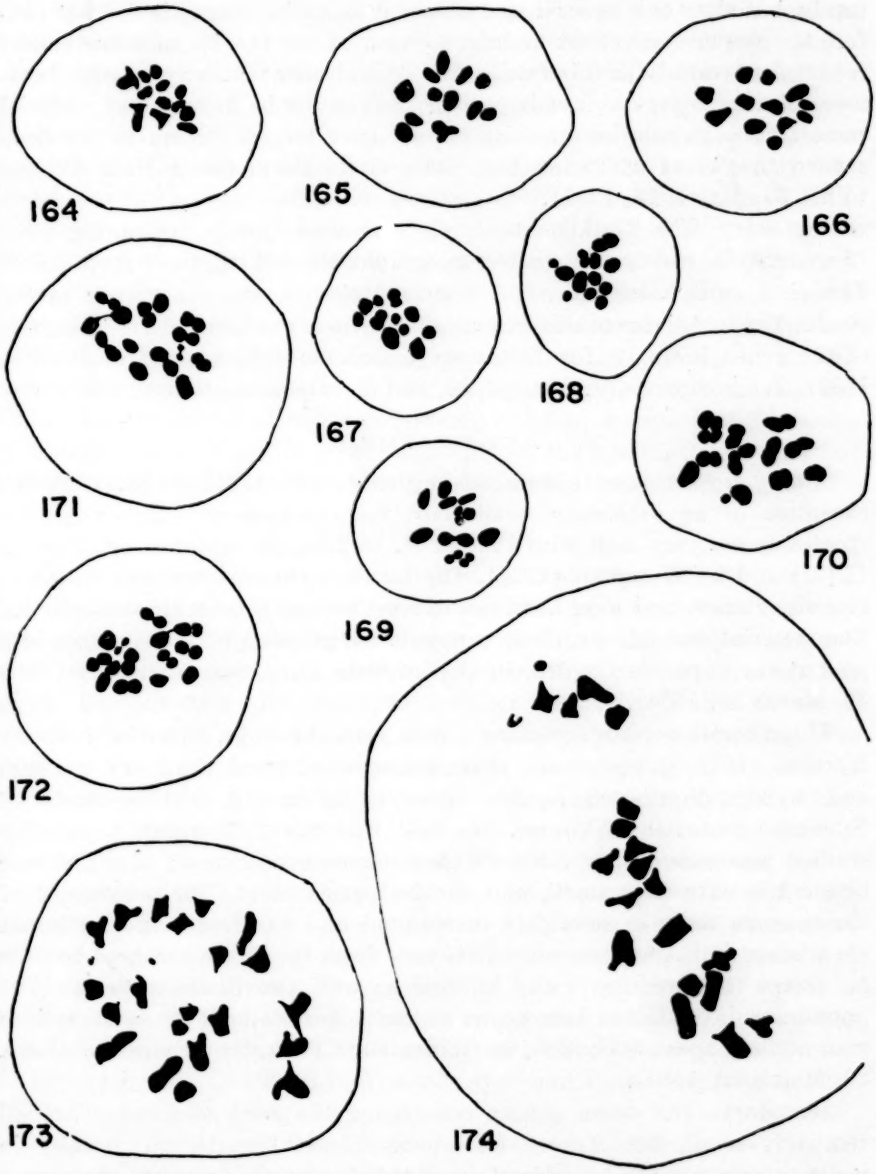

PLATE XVIII. FIGS. 164–166. *Porothamnium bigelovii* ($n = 12$), polar view of first meiotic metaphases, from early to median. FIGS. 167–169. *Claopodium whippleanum* ($n = 11$), polar view of first meiotic metaphases. FIGS. 170–172. *Amblystegium juratzkanum* ($n = 13$), polar view of first meiotic metaphase. FIGS. 173 and 174. *Hygroamblystegium irriguum* ($n = 20$). FIG. 173. Late diakinesis-early metaphase stage. FIG. 174. Side view of first meiotic metaphase. All figures $\times 2160$.

turely, but since this process was observed in all its stages, it did not confuse the chromosome count unduly. In view of the few chromosome counts reported previously in this family, for several very distantly related Japanese species, no cytotaxonomic conclusions can yet be drawn. Our material came from a population growing on soil over large boulders in the deep shaded canyon of a stream, Big Basin State Park, Santa Cruz County (VSB 37, March 18, 1953).

Summary. The Thuidiaceae, a medium sized family containing some 15 genera, is widely distributed geographically. With the exception of *Thuidium,* with more than 150 described species, the genera are rather small. The only chromosome number previously reported for members of the genus is $n = 10$, for *Thuidium japonicum* (Shimotomai & Koyama 1932), *T. viridiforme, T. micropteris,* and *T. uliginosum* (Yano 1951).

Amblystegiaceae

Amblystegium juratzkanum Schimp. (figs. 170–172): $n = 13$. With the exception of an extremely small pair, the chromosome number of this species agrees very well with that of *A. serpens,* as reported by Marchal (1912) and by Wettstein (1924). The bivalent chromosomes fall into several size classes, and were observed to tend toward premature dissociation. The material was collected from a population growing on moist stones in a pool at the Japanese Garden, in Golden Gate Park, San Francisco (VSB 33, March 19, 1953).

Hygroamblystegium irriguum (Wils.) Loeske (figs. 173–174): $n = 20$. Marchal (1912) reported the chromosome number of this very common and widely distributed aquatic moss to be $n = 12$, on the basis of European material, of course. We find that the Californian population studied possesses a very different chromosome complement, of which one bivalent is extremely small, and divides prematurely. The occurrence of chromosome races in so widely distributed and variable a species is not surprising, and American specimens vary from the European type to such an extent that we may really be dealing with two distinct species. The population investigated here grows at and below water level on rocks in a pool at the Japanese Garden, in Golden Gate Park, San Francisco (LEA 32, March 19, 1953).

Summary. The dozen genera comprising the Amblystegiaceae are all relatively small, but of very wide geographical distribution, usually in moist to very wet habitats. Members of this family may attain a very great abundance in bogs, swamps, and pools, and may even become the dominant vegetation there. *Amblystegium serpens* was used as experimental material both by the Marchals (1911, 1912) and by Wettstein (1924), and through apospory, a series of polyploid chromosome races was produced,

with the chromosome numbers, $n = 24$ ($2n$) and $n = 48$ ($4n$). Vaarama has reported for this same species the chromosome number, $n = 22$, from populations from Finland (1950b) and from California (1953b). Marchal (1912) reported chromosome numbers for species in two other genera, *Hygroamblystegium irriguum* ($n = 12$; as *Amblystegium*) and *Leptodictyum riparium* ($n = 24$; as *Amblystegium*). Moutschen (1952) has recently confirmed Marchal's count for *Amblystegium riparium,* and has induced autopolyploidy in this species by means of colchicine. Heitz (1928) has given estimates of the chromosome number of *Calliergonella cuspidata* as $n =$ "(9)10"; of *Calliergon richardsonii* as $n = 20$; and of *Campylium stellatum* as $n =$ "6–8." Vaarama (1950b, 1953b) has reported the chromosome numbers of three species of *Drepanocladus: D. fluitans,* $n = 22$; *D. exannulatus* and *D. uncinatus,* $n = 12$. This family, like most aquatic and semiaquatic groups of plants, is considered to be an unusually difficult one by botanists because of the great variability of the species under differing environmental conditions with resulting taxonomic confusion.

Brachytheciaceae

Homalothecium nevadense (Lesq.) Ren. & Card. (figs. 175–180): $n = 12$. The chromosomes of this species are distinguished not only by the two very small pairs, but also by the fact that several of the normal bivalent chromosomes seem quite constantly to absorb the stain to a lesser degree than others. Consequently, division figures rather characteristically presented an odd appearance of deeply and lightly stained chromosomes. This phenomenon was seen in several capsules, thus removing the chance that it might represent the idiosyncracy of some individual sporophyte. Furthermore, the chromosomes appeared to be somewhat diffuse and not as sharply delimited as in the other mosses studied. Whether this behavior was caused by the methods used in fixing and staining, or whether by some condition inherent in the species, we are unable to say, since similar phenomena were not observed elsewhere. Vaarama (1950b) remarks that the matrix of the chromosomes of *Brachythecium* appears to be less firm than usual, so that the bivalents tend to stick together very commonly. The material was collected from a population that abounds on huge, mist-swept boulders at the foot of Bridal Veil Falls in Yosemite National Park, Mariposa County (WCS 69, April 20, 1953).

Summary. With more than 20 genera, the Brachytheciaceae occur in all parts of the world, although most commonly and abundantly in the more temperate climates. Containing over 200 species, *Brachythecium* is by far the largest genus, although *Rhynchostegium* contains more than 100 species. Chromosome numbers for six species of *Brachythecium* have been reported, as follows: *B. albicans,* $n = 9$, *B. populeum,* $n = 9$, 10, *B. salebro-*

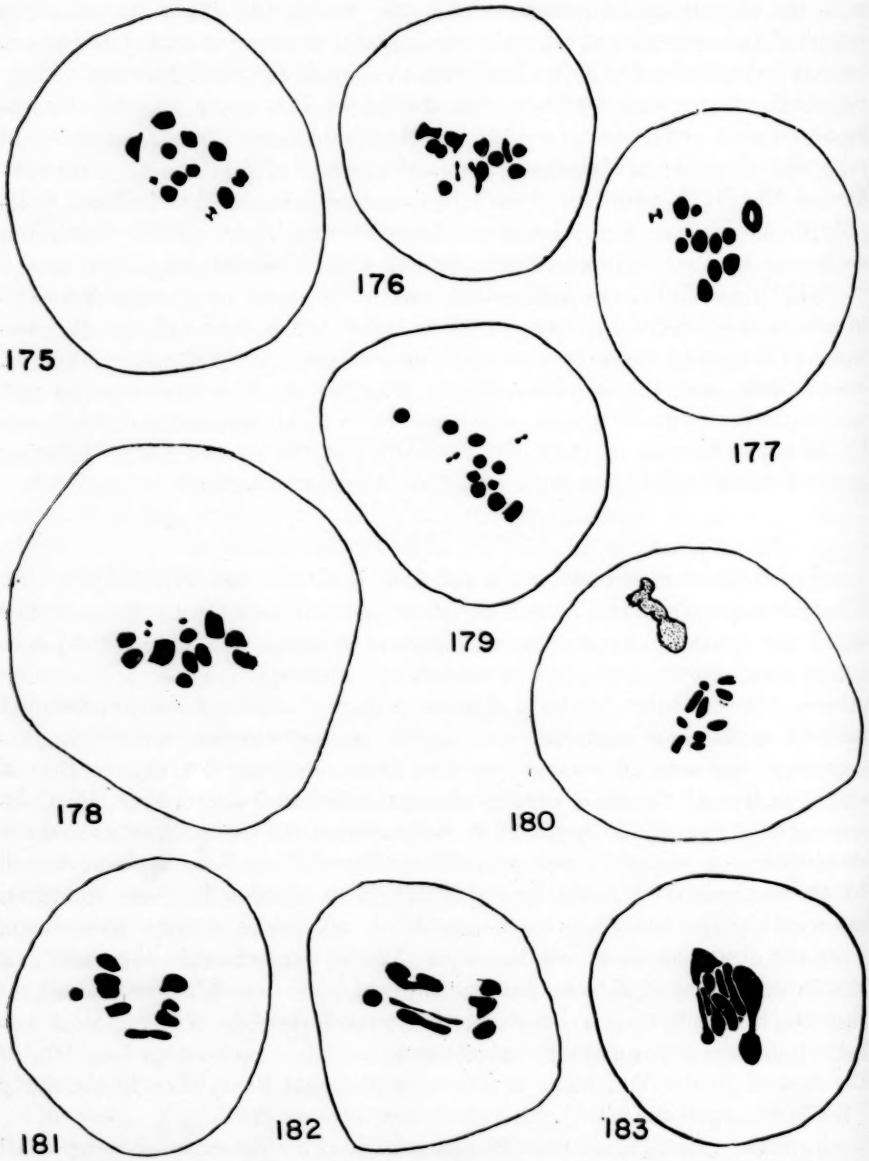

PLATE XIX. FIGS. 175–180. *Homalothecium nevadense* ($n = 12$). FIGS. 175–179. Various stages of first meiotic metaphase, from very early to median, to show behavior of minute pairs of "accessory" chromosomes. FIG. 180. Polar view of second metaphase, showing minute chromosome dividing; one chromosome plate in side view. FIGS. 181–183. *Atrichum undulatum* (California race, $n = 7$). FIGS. 181 and 182. Metaphase stages of first meiotic division. FIG. 183. Anaphase of first division, showing heteromorphic chromosomes. All figures $\times 2160$.

sum, $n = 13$, *B. starkei* ssp. *curtum*, $n = 20$, *B. velutinum*, $n = 11$ (Vaarama 1950b), and *B. rutabulum*, $n = 11$ (Sinoir 1952). Heitz (1928) has estimated the chromosome number of *Eurhynchium rusciforme* as $n = 6–8$; of *E. schleicheri* as $n = 8(9)$; and of *Scleropodium purum* as $n = 9–11$. As already noted, this family seems to be characterized cytologically by the difficulties it presents in the fixing and staining of chromosomes.

Polytrichaceae

Atrichum undulatum (Hedw.) Beauv. (figs. 181–183): $n = 7$. The moss reported upon here is a very common one in the Coast Ranges of California, where it has rather generally been called *A. undulatum* (Koch 1950), although Lesquereux (1868) reported what is undoubtedly the same thing, from "Banks, Santa Cruz Mts., alt. 2,200 ft.," as *A. angustatum* (Brid.) Br. & Sch. However, it should be pointed out that this species is neither *A. undulatum* nor *A. angustatum*, as it differs from the former in being clearly dioecious, in its chromosome number (Lowry 1948, Sinoir 1952), and in the very low and inconspicuous lamellae on the upper surface of the leaf; and from the latter in the broad, strongly undulate leaves, with a relatively narrow costa. Very young plants offer a remarkable resemblance to *A. crispum*, in the short, broad, obtuse leaves. Older leaves develop conspicuous undulations as well as spines on the dorsal surface, which preclude any possibility that it may be *A. crispum*. Some possibility exists that this species may be identical with one already described from the Orient or even from tropical America. Since a final identification of this species is certain to be a time-consuming and laborious task, we have decided to continue using the name, *Atrichum undulatum*, because of its previous application to our material, but with the understanding that some other name will eventually have to be applied to it.

The chromosomes are clearly in 7 pairs, with one larger and obviously dimorphic bivalent. Our material was collected in the Coast Range west of Stanford University, on a soil bank along Alpine Road near its junction with Page Mill Road, at an altitude of over 1000 feet (WCS 44, March 31, 1953). An interesting feature of this collection was the production, in late March, of occasional young sporophytes, accompanying numerous older, deoperculate sporophytes. The long drought in early winter of 1953 and its termination through the resumption of winter rains apparently enabled a new crop of sporophytes to develop, quite out of season.

Summary. Of the more than a dozen genera of Polytrichaceae, a family of large and conspicuous mosses, only three have been investigated cytologically. The chromosome numbers of seven species of *Polytrichum*, nine species of *Pogonatum* and three species of *Atrichum* have now been reported, and distinct cytotaxonomic significance appears in the fact that

TABLE I. *Chromosome numbers in fifty-five species of Californian Musci (Names in italics represent first reports)*

Name and source of material	Reference Numbers	Chromosome Number	Figures
Fissidentaceae			
Fissidens limbatus Sull.			
Stanford University, Santa Clara Co.	LEA 1	$n = 5$	1–4
Fissidens pauperculus Howe			
Muir Woods, Marin Co.	LEA 53	$n = 12$	5–7
Ditrichaceae			
Ceratodon purpureus (Hedw.) Brid.			
Big Basin State Park, Santa Cruz Co.	WCS 43	$n = 13$	8–10
Yosemite National Park, Mariposa Co.	VSB 55	$n = 13$	
Ceratodon purpureus fo. *xanthopus* (Sull.) Britt.			
East of Tomales, Marin Co.	WCS 57	$n = 13$	11
Ditrichum schimperi (Lesq.) Paris			
Muir Woods, Marin Co.	LEA 59	$n = 26$	12–13
Pleuridium bolanderi C. Müll.			
Hedgpeth Ranch, Sonoma Co.	WCS 12	$n = 26$	14–16
Dicranaceae			
Anisothecium varium (Hedw.) Mitt.			
Stanford University, Santa Clara Co.	LEA 2	$n = 14$	17–19
Dicranoweisia cirrata (Hedw.) Lindb.			
Big Basin State Park, Santa Cruz Co.	WCS 31	$n = 11$	20–22
Encalyptaceae			
Encalypta vulgaris Hedw. var. *mutica* Brid.			
Mt. Hamilton, Santa Clara Co.	WCS 39	$n = 13$	23–25
Pottiaceae			
Aloina ambigua (BSG.) Limpr.			
Stanford University, Santa Clara Co.	LEA 6	$n = 24$	26–28
Barbula brachyphylla Sull.			
Mt. Hamilton, Santa Clara Co.	WCS 45	$n = 12$	29–30
Barbula convoluta Hedw.			
Searsville Lake, San Mateo Co.	WCS 36	$n = 11$	31–32
Barbula vinealis Brid.			
Stevens Creek, Santa Clara Co.	WCS 8	$n = 14$	
San Mateo County Park	VSB 19	$n = 14$	33–34
Desmatodon hendersonii (Ren. & Card.) Williams			
Alum Rock State Park, Santa Clara Co.	WCS 51	$n = 13$	35–37
Phaseum cuspidatum Hedw. var. *americanum* R. & C.			
Hedgpeth Ranch, Sonoma Co.	WCS 13	$n = 29–30$	41–43
Mt. Hamilton, Santa Clara Co.	WCS 41	$n = 26$	38–40
Pottia davalianum (Smith) Steere			
Stanford University, Santa Clara Co.	LEA 7	$n = 30$	44–45
Timmiella vancouveriensis Broth.			
Muir Woods, Marin Co.	WCS 58	$n = 14$	46–48
Tortula bolanderi (Lesq.) Howe			
Searsville Lake, San Mateo Co.	VSB 38	$n = 13$	49–50
Tortula laevipila (Brid.) Schwaegr.			
Alpine Road, San Mateo Co.	VSB 47	$n = 12$	51–52
Tortula muralis Hedw.			
Stanford University, Santa Clara Co.	WCS 5	$n = 48$	53–54
Tortula princeps De Not.			
Mt. Hamilton, Santa Clara Co.	VSB 52	$n = 12$	55–57
Stevens Creek, Santa Clara Co.	WCS 5a	$n = 24 + 1$	58–59
Hedgpeth Ranch, Sonoma Co.	WCS 15	$n = 36 + 2$	60–61
Tortula subulata Hedw.			
Yosemite National Park, Mariposa Co.	WCS 71	$n = 49$	62–63

TABLE I (continued)

Name and source of material	Reference Numbers	Chromosome Number	Figures
Weissia viridula Hedw.			
Searsville Lake, San Mateo Co.	VSB 26	$n = 13$	64
Mt. Tamalpais, Marin Co.	WCS 75	$n = 13$	65–66
Grimmiaceae			
Grimmia alpestris (Web. & Mohr) Nees			
Yosemite National Park, Mariposa Co.	WCS 72	$n = 13$	67–70
Grimmia apocarpa Hedw.			
Mt. Hamilton, Santa Clara Co.	VSB 40	$n = 13$	71–73
Yosemite National Park, Mariposa Co.	WCS 70	$n = 13$	74–75
Grimmia pulvinata (Hedw.) Smith			
Stevens Creek, Santa Clara Co.	WCS 9	$n = 13$	
Mt. Diablo, Contra Costa Co.	LEA 28	$n = 13$	76–77
Grimmia trichophylla Grev.			
Mt. Diablo, Contra Costa Co.	VSB 29	$n = 13$	78–79
Rhacomitrium depressum Lesq.			
Yosemite National Park, Mariposa Co.	WCS 67	$n = 14$	80–82
Funariaceae			
Funaria hygrometrica Hedw.			
Hedgpeth Ranch, Sonoma Co.	WCS 11	$n = 28$	83–84
Funaria muhlenbergii Turn. var. *patula* BSG.			
Alum Rock State Park, Santa Clara Co.	VSB 50	$n = 28$	85
Bryaceae			
Bryum argenteum Hedw. var. *lanatum* BSG.			
Hedgpeth Ranch, Sonoma Co.	WCS 4	$n = 12$	86–88
Bryum capillare Hedw.			
Stanford University, Santa Clara Co.	LEA 3	$n = 10+$	89–91
Bryum pseudotriquetrum (Hedw.) Schwaegr.			
East of Tomales, Marin Co.	LEA 61	$n = 11$	92–95
Epipterygium tozeri (Grev.) Lindb.			
Stanford University, Santa Clara Co.	WCS 17	$n = 11$	96–99
Alpine Road, San Mateo Co.	WCS 48	$n = 11$	
Orthodontium gracile Schwaegr.			
La Honda Road, San Mateo Co.	LEA 22	$n = 12$	104–107
Pohlia longibracteata Broth.			
San Mateo County Park	VSB 18	$n = 12$	100–103
Mniaceae			
Leucolepis menziesii (Hook.) Steere			
San Mateo County Park	LEA 21	$n = 5$	108–111
Aulacomniaceae			
Aulacomnium androgynum Schwaegr.			
Big Basin State Park, Santa Cruz Co.	VSB 42	$n = 12$	112–114
Bartramiaceae			
Anacolia menziesii (Turn.) Paris			
West of Saratoga, Santa Clara Co.	WCS 34	$n = 8$	115–118
Anacolia menziesii var. *baueri* (Hpe.) Paris			
Mt. Diablo, Contra Costa Co.	VSB 27	$n = 7$	119–121
Hedwigiaceae			
Hedwigia ciliata (Hedw.) Brid.			
Mt. Hamilton, Santa Clara Co.	LEA 46	$n = 11$	122–124
Pseudobraunia californica (Sull.) Broth.			
Hedgpeth Ranch, Sonoma Co.	WCS 20	$n = 11$	125–126
Orthotrichaceae			
Orthotrichum affine Brid.			
Yosemite National Park, Mariposa Co.	WCS 64	$n = 6$	127–129
Orthotrichum bolanderi Sull.			
Searsville Lake, San Mateo Co.	LEA 23	$n = 6$	130–133
Mt. Diablo, Contra Costa Co.	LEA 24	$n = 6$	

TABLE I (continued)

Name and source of material	Reference Numbers	Chromosome Number	Figures
Orthotrichum cylindrocarpum Lesq.			
South of Olema, Marin Co.	WCS 74	$n = 11$	160–165
Orthotrichum lyellii Hook. & Tayl.			
Mt. Diablo, Contra Costa Co.	WCS 25	$n = 6$	134–136
Yosemite National Park, Mariposa Co.	VSB 54	$n = 6$	
Orthotrichum rivulare Turn.			
Stevens Creek, Santa Clara Co.	LEA 10	$n = 11$	146–151
Ukiah, Mendocino Co.	WCS 66	$n = 11$	152–153
Orthotrichum rupestre Schleich.			
Yosemite National Park, Mariposa Co.	LEA 68	$n = 6$	137–139
Orthotrichum rupestre var. globosum (Lesq.) Grout			
Yosemite National Park, Mariposa Co.	WCS 65	$n = 6$	140–142
Orthotrichum tenellum Bruch			
Mt. Tamalpais, Marin Co.	WCS 60	$n = 11$	154–159
Orthotrichum texanum Sull.			
Yosemite National Park, Mariposa Co.	VSB 56	$n = 6$	143–145
Neckeraceae			
Porothamnium bigelovii (Sull.) Fleisch.			
Big Basin State Park, Santa Cruz Co.	LEA 30	$n = 12(11)$	164–166
Thuidiaceae			
Claopodium whippleanum (Sull.) Ren. & Card.			
Big Basin State Park, Santa Cruz Co.	VSB 37	$n = 11$	167–169
Amblystegiaceae			
Amblystegium juratzkanum Schimp.			
Golden Gate Park, San Francisco Co.	VSB 33	$n = 13$	170–172
Hygroamblystegium irriguum (Wils.) Loeske			
Golden Gate Park, San Francisco Co.	LEA 32	$n = 20$	173–174
Brachytheciaceae			
Homalothecium nevadense (Lesq.) Ren & Card.			
Yosemite National Park, Mariposa Co.	WCS 69	$n = 12$	175–180
Polytrichaceae			
Atrichum undulatum (Hedw.) Beauv.			
Alpine Road, San Mateo Co.	WCS 44	$n = 7$	181–183

with very few exceptions the species have the chromosome number, $n = 7$, or some multiple of it (Lowry 1948, Sinoir 1952). The genus *Atrichum* is of special interest as it demonstrates a well-developed polyploid series. *Atrichum angustatum* has the chromosome number, $n = 7$ (Lowry 1948, Tatuno 1951), whereas *A. undulatum* is apparently a diploid or triploid form, with the chromosome number, $n = 14$ or $n = 21$ (Lowry 1948, Kurita 1937). It is of interest to observe the close correlation of dioecism with haploid species (in terms of the gametophyte), and of monoecism with diploid ones, as clearly pointed out in the genus *Mnium* by Heitz (1942) and by Lowry (1948).

Discussion. Chromosome numbers. Even including chromosome numbers for over 50 species of mosses reported in the present paper, the total number of species for which definite chromosome counts have been published still remains considerably below 200, out of about 20,000 described species of mosses. In view of this very small proportion of species whose

chromosome numbers are known compared with those that have not received cytological investigation, it would be premature to make any large-scale generalizations at this time. However, some very general conclusions can be reached, even if the details may be considerably changed as studies on chromosome behavior in mosses continue. Compared with pteridophytes (Manton 1950), the chromosome numbers in bryophytes are relatively small,

TABLE II. *Frequency of occurrence of chromosome numbers among moss species*

Chromosome Number	Number of Species	Chromosome Number	Number of Species
5	3	20	5
6	23	21	2
7	26	24	4
8	7	25	1
9	4	26	5
10	12	28	7
11	21	30	2
12	25	36	1
13	17	48	1
14	14	49	1
15	2	52	1
16	3	60	1
18	2	66	1

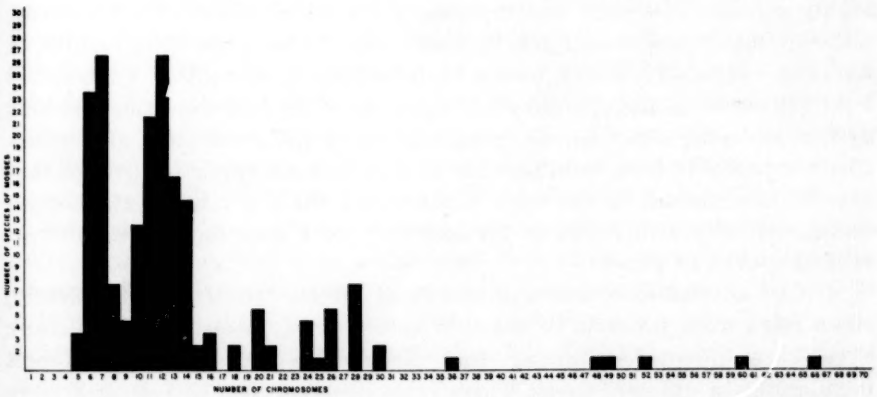

TABLE III. *Graphical representation of chromosome number frequency in mosses, based on all published reports of definite numbers (through 1953), as well as the present investigation.*

and agree surprisingly well with the basic numbers found in flowering plants. The lowest chromosome number yet found in mosses is $n = 5$, reported previously for only two species, *Mnium* (*Leucolepis*) *menziesii* (Lowry 1949) and for *Hylocomium* (*Pleurozium*) *schreberi* (Vaarama 1950b). The present investigation substantiates the count for *Leucolepis menziesii* and adds *Fissidens limbatus* to the list of those with five pairs.

The highest numbers of chromosomes yet known in mosses have been reported by Vaarama (1953b), for *Tortula muralis,* where $n = 60$ and $n = 66$, and for *Phascum cuspidatum,* where $n = 52$. In the course of the present investigation, high chromosome numbers were found in *Tortula muralis* ($n = 48$) and in *T. subulata* ($n = 49$). All these species with high chromosome numbers belong to the same family, the Pottiaceae, in which lower chromosome numbers are also found. The Mniaceae seem to display consistently the lowest numbers of chromosomes for a whole family, with the basic numbers, $n = 6$, $n = 7$, and $n = 8$, and their multiples, except for *Leucolepis menziesii,* already mentioned, in which $n = 5$. A summary of the chromosome numbers so far definitely reported for mosses, excluding estimates, and including the present investigation, shows several interesting features (Table II). An interesting feature of this table is the unexpectedly clear polymodality of chromosome numbers in mosses, a condition that will probably be emphasized by future work, rather than reduced. The numbers, $n = 6$ and $n = 7$, occur in almost equal frequency, in 23 and 26 species, as do the numbers $n = 11$ and $n = 12$, in 21 and 25 species. Smaller modes are found at $n = 20$, with five species, $n = 25$, with four species, and $n = 26$ and $n = 28$, with five and seven species, respectively. Because of the unexpected clearness of the modes in this preliminary analysis, it seems highly possible that each one represents a level of ploidy. Consequently, although many species and genera would seem to have the basic number of $n = 10$, $n = 11$, $n = 12$, $n = 13$, or $n = 14$, these may be already at a tetraploid level (in terms of the sporophyte). Since the autoploid condition presents certain advantages to the moss gametophyte, as discussed later, this condition has probably been stabilized for so long in some species or groups that now it does amount to the basic number. On the other hand, further investigation may still result in the discovery of a true haploid number in related species or genera.

Before chromosome counts in species of mosses can be accepted finally, much more work needs to be done. Within species, inconsistencies already have been discovered among the chromosome numbers of different populations in different areas. There is no question that chromosome races exist in nature, as shown for *Timmia cucullata* by Lowry (1953), for *Tortula ruralis* and *Orthotrichum tenellum* by Vaarama (1953a, b) and for *Atrichum undulatum* by Heitz (1926, 1928). Further examples can be cited from the present investigation, as *Phascum cuspidatum* and *Tortula princeps.* The identification of Californian moss populations with European species may occasionally result in considerable straining of specific concepts, as suggested by the fact that several of the California mosses have different chromosome numbers than the European species under whose names they pass, as *Phascum cuspidatum* ($n = 26$ or 29–30 in California,

$n = 52$ in Finland), *Weissia viridula* ($n = 13$ in California, $n = 14$ in Finland), *Grimmia apocarpa* ($n = 13$ in California, in two populations; $n = 12$ in Finland), *Funaria muhlenbergii* ($n = 28$ in California, $n = 26$ in Europe), *Bryum argenteum* ($n = 12$ in California, $n = 10$ in Europe), *Bryum pseudotriquetrum* ($n = 11$ in California, $n = 10$ in Europe), *Mnium pseudopunctatum* ($n = 14$ in Michigan, $n = 13$ in Europe), *Hedwigia ciliata* ($n = 11$ in California, $n = 22$ in Finland), and *Hygroamblystegium irriguum* ($n = 20$ in California, $n = 12$ in Europe). As a consequence of the foregoing considerations, a chromosome number reported from a single area or a single population, although in itself a significant datum, cannot be accepted finally as the chromosome number of the species throughout its whole geographic range.

Chromosome studies of the somatic tissues of the gametophyte of mosses present the advantages, as shown by Lowry (1948), that morphological distinctions are generally much more obvious than in the more contracted meiotic chromosomes, and that the presumably haploid chromosome number is encountered there, free of the complications often found at meiosis. An additional point of interest, apt to be overlooked, is that the gametophyte population is usually clonal. With very few exceptions the sexual plants are long-lived, and they are generally provided abundantly with some means for vegetative reproduction, as from the continued growth of the original protonemata, from the repeated growth and branching of the plants themselves, from regeneration of almost any cell of the stem or leaf, and from specialized cellular structures of various types, as gemmae and propagula, that result in the rapid propagation of the green plants. In some species, perhaps because of the success of vegetative propagation, sporophytes are rarely or never produced. The sporophytes, however, can not be members of clones, strictly speaking, since each one results from a separate fertilization, and so is homologous to a whole seed plant. However, because of the large expanses of a single gametophytic clone, especially if it is monoecious, the parentage of the sporophytes is probably very uniform, although no studies on this problem in nature have been undertaken. Nevertheless, since each sporophyte can have a somewhat different genotype, if accidents of fertilization so dictate, considerable variation in genetic stability can be expected. The discovery by Vaarama (1953a) of two chromosome races in the two sporophytes of *Orthotrichum tenellum* he studied and our finding of three chromosome races in three populations of *Tortula princeps* might indicate a considerable degree of hybridization with a possible impact on chromosome numbers and speciation.

Polyploidy. It should be recalled here that the first polyploid series known in plants was created artificially in mosses through apospory. The discovery by Pringsheim (1878) that the young sporophytes of several

species of mosses would regenerate gametophytic tissues was so far ahead of his time that its importance was not then properly appreciated. With the realization of the cytological differentiation of sporophyte and gametophyte and of the alternation of a haploid sexual generation with a diploid asexual generation by Strasburger (1894), the significance of apospory was finally understood. The brilliantly conceived and executed researches of the Marchals resulted in the experimental production of a tetraploid race ("var. *bivalens*") of *Bryum capillare* (Marchals 1911) and of tetraploid and octaploid ("var. *bivalens*" and "var. *quadrivalens*") races of *Amblystegium serpens* (Marchals 1911, 1912). Wettstein and others, in more modern investigations (1923–1924), succeeded in producing autoploid and amphiploid races in several mosses, including *Funaria hygrometrica* ($n = 14$, $n = 28$, $n = 56$), *Physcomitrium piriforme* ($n = 18$, $n = 36$, $n = 72$), *Bryum caespiticium* ($n = 10$, $n = 20$), and *Amblystegium serpens* ($n = 12$, $n = 24$). Heitz (1945) was able to produce polyploidy in *Aulacomnium androgynum* through the action of colchicine, although the chromosome numbers were not established definitely. Moutschen (1952) obtained similar results in *Amblystegium riparium* with colchicine. The discovery of polyploids in natural populations was much delayed, however, largely because of the technical problems already outlined. The first instance of polyploidy in mosses, in nature, seems to be represented by the report by Heitz (1926) of a diploid (in terms of gametophyte) race of *Atrichum undulatum* with the chromosome number of "14–16," and his subsequent report (1928) of a triploid race with the number "(20)21(22)." Later (1942), Heitz elaborated on this thesis to some extent, and pointed out the existence in nature of paired species, one diploid and the other tetraploid, as *Mnium spinosum* and *M. spinulosum, Mnium orthorhynchum* and *M. marginatum, Mnium punctatum* and *M. pseudopunctatum*. He further showed an interesting relationship between such paired species, that the haploid species are heterothallic and that the diploid species are homothallic, indicating a strong possibility that the diploid species arose through sporophytic regeneration or apospory. Of course, there is equal possibility that such races have arisen through unreduced spores, and occasional giant spores are seen in mosses. Vaarama (1949) has reported the occurrence of polyploid areas in the archesporium of *Rhacomitrium ramulosum* and of *Grimmia muhlenbeckii,* which could give rise to diploid spores. It is clear that diploid sectors or chimeras of the gametophytic moss plant would still retain the sex of the haploid parent tissue, and would be genetically unable to produce a monoecious plant. This fact lends some strength to Heitz's hypothesis that natural apospory has been effective in producing diploid races or species of mosses. Since these paired diploid species have not yet been reproduced in the laboratory through the experimental in-

duction of apospory, we still do not know whether in nature they arose long ago and have undergone further evolution to reach their clear-cut isolation as species, or whether they have been produced repeatedly from time to time, up to the present. The latter possibility presents a very striking and unique means of polyphyletic speciation, by which all populations comprising a species might not be related, except in terms of the parent species. Lowry (1948) has confirmed most of Heitz's findings, and has reported other cases of paired species in *Mnium*, of the same type, as well as haploid and diploid races (in terms of the gametophyte) within *Mnium cuspidatum*. As already indicated, we have found that a California population in *Hedwigia ciliata* has the chromosome number, $n = 11$, without doubt, whereas the same species has been reported from Finland as having the number, $n = 22$ (Vaarama 1950b). Furthermore, we have found diploid ($n = 12$), tetraploid ($n = 24 + 1$) and hexaploid ($n = 36 + 2$) races of *Tortula* princeps, out of the three races studied, raising some interesting speculations on what further investigations of this handsome species will bring to light. Other examples of natural polyploidy, although at a somewhat different level, can be cited. Lowry (1953) has demonstrated that a population of *Timmia cucullata* in southern Michigan has the chromosome number, $n = 16$, whereas a population from Wisconsin, studied in considerable detail by Scheuber (1932), is reported to have the chromosome number, $n = 12$. Another example of this type is given by *Tortula muralis*. In two populations from Berkeley, Vaarama (1953b) found chromosome numbers of $n = 60$ and $n = 66$, whereas a population at Stanford University has the number, $n = 48$. Again, the future of investigations on this species would seem very promising, for obvious statistical reasons.

The surprisingly large proportion of species that are apparently tetraploid or of higher ploidy, shown by Table II and its extension in graph form, is reflected by cytological behavior. Multiple associations of chromosomes at meiosis were observed occasionally to regularly in several species, notably *Timmiella vancouveriensis* (fig. 48) and *Bryum capillare* (fig. 90). Quadripartite chromosomes were observed from time to time at the first anaphase, and a clear case of multiple association at the second division was seen in *Bryum argenteum* var. *lanatum* (fig. 88), but not well understood. One of the most common evidences of polyploidy in species with apparent basic numbers of 10, 11, 12, 13 and 14, is the obvious duplication of chromosomes, and their tendency to remain in proximity, even into the second division. The prevalence of tetraploid species in which the basic number appears to be an odd one, especially $n = 11$ or $n = 13$, seems to be explained by the usual presence of one or more larger "pairs" which give evidence of being multivalent structures. *Ceratodon purpureus* offers an excellent example, in which the large sex chromosome (Heitz 1932, Ja-

chimsky 1935) is accompanied by 12 autosomes of about the same size. The rather clear secondary pairing of autosomes (figs. 8, 9) would seem to indicate that the present chromosome number, $n = 13$, may well have been derived from an original number, $n = 14$, or from the hybridization and subsequent doubling at some remote past time of two species with the chromosome number, $n = 7$. In highly polyploid members of the Pottiaceae, many of the chromosomes at the first metaphase, in polar view, appear to be in rows or in chains, probably reflecting the mutual attraction of duplicated chromosomes (figs. 53, 54 and 61).

The original, truly haploid, chromosome number of mosses is of course impossible to determine at present, at least without comprehensive genetical work. However, there seems to be some evidence for the view that the most frequent basic numbers so far encountered, $n = 6$ and $n = 7$ (Table II) may themselves represent chromosome duplication in whole or in part. Many of the excellent figures given by Lowry (1948), of somatic chromosomes from the gametophyte of different species of *Mnium* with the basic number, $n = 6$, show more than a suggestion of such duplication, not only in shape and size, but also in orientation. Lowry's table of chromosome length (1948) does not offer much positive evidence for such a view, however, since in only one species did he find two chromosomes of the same length. An apparent duplication of chromosomes is also seen occasionally at meiosis in species with low basic numbers, as in *Orthotrichum rupestre* (fig. 137). If the gametophyte of mosses is genuinely haploid, then the genes cannot occur in allelomorphic pairs, but would have been segregated at meiosis.

Aneuploidy. Most reports of aneuploidy in mosses seem to represent races derived from chromosome fragmentation, as shown most graphically in *Orthotrichum tenellum* by Vaarama (1953a). A few aneuploid races may possibly be indicated by reports of varying chromosome numbers in the same species by different authors, although the chance of error or misinterpretation of chromosome counts cannot be overlooked, especially in early investigations, before the development of adequate techniques. For example, earlier workers reported the chromosome number, $n = 6$, in *Polytrichum commune* (Woodburn 1915), *Polytrichum juniperinum* (Allen 1912), and *Polytrichum piliferum* (Vandendries 1912), whereas recent investigations (Vaarama 1950b) show the chromosome number of these three species to be $n = 7$. In these examples, we are undoubtedly dealing with the results of refinement of technique rather than aneuploid races. Other disagreements in published chromosome counts, where the European population differs from the American one, have already been listed. These differences may be due as much to overextension of specific or varietal limits as to true intraspecific aneuploidy. However, an outstanding example of

true aneuploidy was discovered in the course of the present investigation, in *Phascum cuspidatum* var. *americanum,* in which a race from Mt. Hamilton, Santa Clara County, has the chromosome number, $n = 26$ (figs. 38–40), whereas a race from Sonoma County has the number, $n = 29$ and 30 (figs. 41–43). These races have been isolated geographically for long periods of time, since they occur in separate mountain ranges, within the system of the Coast Range. The chromosomes differ not only in number, but in the presence of two pairs of very minute chromosomes in the Sonoma County race. It seems safe to predict that further examples of aneuploidy as clear as this one will be discovered as chromosome studies on mosses continue.

Chromosome fragmentation may result in races of mosses with different chromosome complements, as beautifully demonstrated by Vaarama's somewhat fortuitous discovery that, of two capsules of *Orthotrichum tenellum* from the same population, one had nine bivalents whereas the other had ten. After an analysis of the bivalents, he offers the following explanation "it seems most probable that the increased bivalent number of sporogone 2 is due to fragmentation of the long A-bivalent present in sporogone 1. The fragmentation has obviously taken place through the submedian constriction present in the A-bivalent, and the two new bivalents formed correspond to the arms of the long chromosome. It may also be stated as likely that the A-bivalent is a fusion product of the two bivalents mentioned present in sporogone 2." A similar situation was discovered in *Weissia viridula,* in which the California population contains thirteen bivalents, whereas the European one is reported to have fourteen bivalents (Vaarama 1950b). Vaarama figures these fourteen bivalents as more or less the same size (his fig. 2a, b), whereas all the sporocytes seen, of the Californian race, contain twelve bivalents of approximately the same size and one very large one (figs. 64–66). It is clear that the fragmentation of this large chromosome would result in a 14-bivalent race—or that the more or less permanent association of two bivalents in the European race would result in the condition seen in the Californian race. A study of somatic chromosomes in these races, both of *Orthotrichum* and of *Weissia,* would be very rewarding, as providing material more suitable for quantitative studies. Lowry (1948) has demonstrated clearly that chromosome fragmentation has taken place in a Michigan race of *Mnium pseudopunctatum,* in which $n = 14$. In this species he found two very minute somatic chromosomes averaging .075 μ in length and two much longer chromosomes, averaging 2.7 μ long, with terminal attachment regions. It would seem clear from this evidence that the minute chromosome represents the short arm and the longer chromosome with terminal attachment represents the longer arm of a J-shaped chromosome with a subterminal attachment, a normal type in *Mnium.* The population studied by Lowry is of especial interest since in

Europe this species is reported to have the chromosome number, $n = 13$ (Heitz 1942, Vaarama 1950b), which would indicate that only one of the J-shaped chromosomes of the pair had fragmented. The discovery by Vaarama (1950b) of races within *Brachythecium populeum* with chromosome numbers of $n = 9$ and $n = 10$ may also be related to chromosome fragmentation.

Accessory chromosomes. Accessory chromosomes or accessory isochromosomes were first reported in Bryophyta by Vaarama, in two species of mosses, *Grimmia muehlenbeckii* (1949) and *Dicranum majus* (1950a). Later, he reported this type of chromosome in *Ulota curvifolia* (1950b) and in *Orthotrichum tenellum* (1953a, b). In the present investigation, very small chromosomes and chromosome pairs, of the kind that Vaarama has called accessory chromosomes, were found regularly in 16 species of California mosses, as follows, *Anisothecium varium* (figs. 17–19), *Aloina ambiguua* (figs. 26–28), *Desmatodon hendersonii* (figs. 35–37), *Phascum cuspidatum* var. *americanum* (the Sonoma County race, figs. 41–43), *Tortula princeps* (figs. 58–61), *Tortula subulata* (figs. 62–63), *Bryum capillare* (figs. 89–91), *B. pseudotriquetrum* (figs. 92–95), *Orthodontium gracile* (figs. 104–107), *Anacolia menziesii* (figs. 115–118), *Orthotrichum rivulare* (figs. 146–153), *O. cylindrocarpum* (figs. 160–163), *O. tenellum* (figs. 154–159), *Amblystegium juratzkanum* (figs. 170–172), *Hygroamblystegium irriguum* (figs. 173–174), and *Homalothecium nevadense* (figs. 175–180). Very minute supernumerary chromatic bodies were observed very rarely in other species that did not seem typically to have accessory chromosomes, but, of course, they could have been overlooked. Such bodies were seen, for example, in one sporocyte of *Bryum argenteum* var. *lanatum* (fig. 87), and in *Orthotrichum bolanderi* in only two of the four anaphase groups following the second meiotic division (fig. 133), in a single sporocyte. There is some possibility that these are the result of chromosome fragmentation in single sporocytes. In still other species, the range of the size of bivalents decreases in a regular scale to the point at which the smallest pairs fall within the size range of the so-called accessory chromosomes, as in *Fissidens pauperculus* (figs. 5–7), *Timmiella vancouveriensis* (fig. 47) and *Tortula bolanderi* (fig. 50), as well as in many others of the obviously polyploid members of the Pottiaceae, *Rhacomitrium depressum* (fig. 82), and *Aulacomnium androgynum* (figs. 112–114).

With the exception of *Bryum capillare,* in which five very minute chromosomes are grouped closely together just before the first metaphase (fig. 89) and are then apparently distributed unequally during anaphase (fig. 91), the so-called accessory chromosomes of the remaining 15 species behaved with some to very great regularity. Except for their very small size and their prevalent tendency to dissociate either before or after the first

meiotic metaphase, they seem to behave reasonably normally as bivalents, and to divide regularly in the second division (fig. 159), so that each spore will contain a minute chromosome representing the original accessory chromosome. As the normal bivalents in mosses seem to demonstrate a considerable amount of precocious dissociation, and as they may also be very small, thus providing a point at which normal bivalents and accessory chromosomes find common ground, we decided to include all chromatic bodies that behaved regularly in the chromosome count. Because of the large number of species which were observed to have accessory chromosomes—more than 25 per cent of the Californian species studied—considerable attention was given to their behavior, as a result of which we find ourselves in some disagreement with Vaarama, especially in his analysis of *Orthotrichum tenellum* (1953a). Vaarama reported the presence of two accessory chromosomes in "sporogone 2," which had 10 normal bivalents, and four accessory chromosomes in "sporogone 1," which had only nine normal bivalents. Although we have not rediscovered the anomalous race represented in Vaarama's "sporogone 1," we have investigated many capsules from a population with 10 bivalent chromosomes, and with what Vaarama has reported as two accessory chromosomes. However, even though some of our evidence may appear to be circumstantial, it is our opinion that these accessories really represent one bivalent structure. Although this tiny bivalent obviously dissociates very early, the orientation of the two parts at the first metaphase certainly conforms to the usual behavior of bivalent chromosomes (figs. 154–156), and their habit of dividing prematurely during the first anaphase (figs. 157–158) definitely parallels the not uncommon behavior of univalent chromosomes. Furthermore, in *Orthotrichum cylindrocarpum,* which is so closely related to *O. tenellum* that it has been considered to be only a variety of it by Koch (1950), the accessory chromosomes appear as a single minute bivalent (figs. 160–163). In *O. rivulare,* which is not particularly closely related to *O. tenellum,* but which has the same chromosome number, the accessory bivalent is obviously double at diakinesis (fig. 146) and at early metaphase (figs. 147–149). At metaphase, its parts disjoin to produce much the same condition as seen in *O. tenellum* (fig. 150). The very similar chromosomal behavior of these three species, except for the exceptionally precocious disjunction of the so-called accessory chromosomes of *O. tenellum,* has led us to the conclusion that in all of them, $n = 11$. Exactly parallel situations may be found in other genera and families, and after a survey of so many species, one can not help but be impressed by the regularity in behavior, rather than the lack thereof, of the accessory chromosomes. A study of the somatic chromosome complements of species with accessory chromosomes at meiosis would now seem to be an urgent necessity. A point of considerable interest

conversely, is that all the species in which accessory chromosomes have been found so far are probably polyploid (Tables II and III). It is also of some significance that accessory chromosomes have not yet been shown to occur in species of mosses with such basic chromosome numbers as $n = 5$, $n = 6$, or $n = 7$. Nevertheless, accessory chromosomes may eventually be discovered to occur at the diploid level in mosses, even if with considerably smaller frequency than in polyploids. This possibility is clearly demonstrated by Cleland's (1951) recent report of the occurrence of "extra, diminutive chromosomes" in two wild races of *Oenothera hookeri* in California. His stimulating discussion of the possible methods by which such chromosomes might arise is certainly applicable to the situation in mosses.

Sex chromosomes. Sex chromosomes were first discovered in plants in the hepatic, *Sphaerocarpos* (Allen 1917), on a presumptive basis, at first, but later they were demonstrated to be the sex-determining mechanisms through long-continued and fruitful genetic experiments (Allen 1945). However, in many other dioecious bryophytes, larger and usually dimorphic chromosome pairs have been called sex chromosomes without further proof, and have been so accepted in the literature. It should be pointed out that any such report of sex chromosomes, without genetical proof, can be only an assumption or an hypothesis. In mosses, sex chromosomes have been reported in perhaps a dozen species by Heitz (1932), Shimotomai and Koyama (1932), Shimotomai and Kimura (1936), Jachimsky (1935), Vaarama (1950a), and Tatuno (1951). In the course of the present investigation, dimorphic chromosomes were observed distinctly in *Ceratodon purpureus* (figs. 8–11), *Weissia viridula* (figs. 64–66), *Leucolepis menziesii* (figs. 109–111) and in the Californian race of *Atrichum undulatum* (fig. 183). In many other species, dimorphic chromosomes were observed at certain stages of the first meiotic division, but not so constantly or as conspicuously as in those just listed. A detailed investigation of heterochromosomes in Californian mosses should be rewarding, because of the large number of dioecious species, and the many indications of interesting phenomena seen in our preliminary observations. The otherwise excellent work of Ernst-Schwarzenbach on sexual dimorphism and heterospory in *Macromitrium* (1944) leaves untouched this aspect of the chromosomal situation which would appear to be a central part of the whole problem. The sexual dimorphism in the gametophytes of some mosses is remarkable in that the male plant is reduced to an almost microscopic, bud-like structure that is epiphytic on the large female plant, recalling the nannandrous condition of some species of *Oedogonium*. The only species of this sort that has been studied cytologically is *Dicranum majus* (Vaarama 1950a), in which a complicated chromosomal situation was discovered, including a large bivalent assumed to be the site of the sex-determining genes.

Meiotic features. Unlike the situation reported in previous papers (Vaarama 1949, 1950b), we found prophase stages of meiosis very abundantly in the Californian populations, including well-marked stages of diakinesis. In California, the sporophytes of most mosses mature in late winter and early spring, when the cold nights, especially at higher altitude, must cause the suspension of meiosis. In the present investigation, it was observed that the sporocytes of mosses brought in from the field early in the day were often in late prophase or tetrad stages. Exposure to light and warmth, however, induced the young sporocytes to resume meiosis. In view of the many chromosomal aberrations noted at the first and second meiotic divisions, a careful study of prophase behavior is urgently needed, especially of pachytene stages.

Premature disjunction and division. One of the serious problems in counting the chromosomes of mosses is the precocious dissociation of bivalents. As already outlined under the discussion of several highly polyploid members of the Pottiaceae, the counting of chromosomes in some species must amount to an estimate rather than an exact count, because of the high proportion of univalent chromosomes at the first division. Occasional cells are seen in which all the bivalents have dissociated before the first metaphase, as in *Fissidens limbatus* (figs. 3 and 4). Fortunately, the univalents can be identified with some certainty because of their smaller size (compare figs. 1 and 2 with 3 and 4). If it were not for the smaller size of the chromosomes where double the usual number is present, one could interpret these as polyploid cells. At the anaphase of the first division, the univalent chromosomes may divide prematurely in preparation for the second division, to such an extent that accurate counts might be jeopardized were it not for the proximity and the orientation of the chromosomes. Vaarama (1950b) reported behavior of this sort in *Weissia viridula,* and we have observed the same phenomenon in several species, most notably in *Pseudobraunia californica* (fig. 126). In occasional figures of some species, the first anaphase chromosomes clearly show a quadripartite nature, either as the result of long established polyploidy or in preparation for the first somatic division of the spore, a point that was not resolved. The double nature of the chromosomes at the first anaphase also appears in the metaphase of the second division (fig. 159).

Delayed disjunction. The lagging of chromosomes was observed in many sporocytes, and has been well documented by Vaarama (1949) in members of the Grimmiaceae, as well as in other mosses (1950b). Nevertheless, in observations on thousands of tetrads during the course of this investigation, not one was seen with more or less than four spores, except those in one capsule of *Weissia viridula,* where giant spores and diads were found. It may be that spores containing other than the usual complement abort

or disintegrate after the separation of the four members of each tetrad. The techniques evolved for estimating chromosomal aberrations in higher plants by counting the proportion of fertile to sterile pollen should eventually prove to have some application to mosses.

Satellites. Although undoubtedly present in somatic chromosomes of many species, satellites were seen at meiosis in a single species, *Leucolepis menziesii* (fig. 111), which appears to be the first moss for which these chromosomal features can be reported.

Chiasmata. It was observed that each species has its own fairly constant proportion of bivalents with interstitial and terminalized chiasmata. The constant occurrence in many species of nearly equal numbers of bivalents of the two types would seem to indicate that external factors are not responsible for the inhibition of terminalization, or conversely, were not responsible for conditions aiding the terminalization of chiasmata. Consequently, it is concluded that the nature of chiasmata in the bivalents of mosses, at least in the species investigated, is determined genetically rather than environmentally. Diakinesis stages were found to be especially helpful in interpreting chiasmata, as seen in *Dicranoweisia cirrata* (fig. 20) and *Orthotrichum lyellii* (fig. 134).

Sporocyte size. The spore mother cells varied greatly in size among the species investigated, from 10 μ in diameter in *Fissidens* (figs. 1–7) to more than 40 μ in *Pottia* (fig. 44) and *Pseudobraunia* (fig. 126). No correlation could be seen between the size of sporocytes and other factors, as annual habit, size of plants, dryness or moistness of habitat, number of chromosomes, or total amount of chromatin present. Small sporocytes may have very large numbers of small chromosomes, as in *Tortula muralis* (fig. 53), or a few large chromosomes as in *Atrichum* (figs. 181–183) and *Leucolepis* (figs. 108–111). Conversely, large sporocytes may have a small number of chromosomes, as in *Hedwigia* (figs. 122–124) and *Pseudobraunia* (figs. 125 and 126), or a much larger one, as in *Funaria* (fig. 85).

General conclusions. Investigations on the chromosome behavior of mosses are still too few for any final and detailed conclusion. Nevertheless, some generalizations are possible. For example, in most families in which several representatives have been studied, it becomes clear that the chromosome numbers within the family tend to be related to each other in terms of a basic number or within a rather narrow range of variation. Within genera, likewise, a marked correspondence in the basic chromosome number usually appears, in the few cases where several species in the same genus have been studied. Conversely, the conspicuous deviation from the normal chromosome number in the genus *Mnium* found in *Leucolepis menziesii* establishes a cytological basis for its recognition as a valid segregate genus, as suggested by Lowry (1948). Further studies on chromosome numbers

and behavior in large and taxonomically difficult genera will be especially helpful in interpreting the position of anomalous members of such genera, in establishing the limits of sections and subgenera, and perhaps in estimating the degree of hybridity and genetic stability in the species. However, a great deal of detailed cytological research is necessary before the results of chromosomal studies will be really useful to taxonomists at the specific and subspecific levels. Lowry's detailed investigation of the somatic chromosomes of American populations of several species of *Mnium* represents the first serious cytotaxonomic study of mosses, and establishes the value and utility of such work. Persson (1949) has made some penetrating and thoughtful comments on the lack of morphological and anatomical features of cryptogamic plants, as compared with the phanerogams, that creates many difficulties in distinguishing between vicarious races and species. He even suggests the somewhat metaphysical possibility that different species might appear identical, simply for want of disinguishing features. This question is an appropriate one here, in view of the current assumption, already mentioned, that many European and American moss populations belong to the same species, and the very general application of European names and concepts to American species. However, it has been shown in the present investigation, and to some extent in earlier ones, that the chromosome complement of some of the American populations differs from that of the supposedly identical European species. Thus, the chromosome numbers, morphology, and behavior may furnish useful new criteria for the better understanding of an old problem.

Too few genera and families of mosses have been studied cytologically to enable us to see any clear relationship between chromosomes, either in number or morphology, and phylogeny. The fossil record of bryophytes is almost non-existent, because of the small size and delicate structure of the plants (Steere 1946), so that all phylogenetic arrangements are almost purely speculative, with serious conflicts among them. The high chromosome numbers and numerous polyploid series found in the Pottiaceae represent an advanced feature, in terms of evolutionary specialization. It is still too early to correlate chromosome behavior with annual and perennial habit, as data on annual species is nearly lacking.

From time to time the question arises whether the species of cryptogams are coordinate with or equivalent to the species of higher plants, a problem that has deserved serious consideration by botanists. The cytological behavior of bryophytes, both normal and anomalous, appears to parallel that of phanerogams very closely, as is shown especially well by the existence of polyploid and aneuploid races, the multiple association of chromosomes during the first and second meiotic divisions, the precocious disjunction of bivalent chromosomes and of chromatids, and the presence of so-

called accessory chromosomes, and of sex chromosomes. Finally, it seems safe to conclude that species of mosses, and of bryophytes in general, in spite of their relatively simple morphology, present the same kind and degree of complexity as those of higher plants, and that speciation within natural populations of mosses is governed by the same patterns of cytological behavior.

Summary

1. The chromosome behavior at meiosis of 73 populations of Californian mosses, mostly from the San Francisco Bay region, has been studied.

2. Chromosome numbers were determined for 55 species, representing 39 species, 16 genera, and 2 families whose cytology had not been investigated previously.

3. Previous reports on chromosome numbers of mosses are integrated with the present results, where appropriate, and a general discussion of the significance of chromosome numbers within families is given.

4. Since the chromosome studies were made on temporary mounts, through the use of aceto-orcein and the squash method, voucher specimens have been preserved, with detailed locality data, so that any of the populations may be found again if further investigation is desirable.

5. In the species investigated, a range of chromosome numbers from $n = 5$ to $n = 49$ was found.

6. A graph of the frequency of species with different chromosome numbers is clearly polymodal, with the highest frequencies at $n = 6$–7, $n = 11$–12, $n = 20$, $n = 24$, and $n = 28$, suggesting a high incidence of polyploidy.

7. Polyploidy was encountered within several species, notably in *Tortula princeps,* in which three different populations were found to represent three different stages of polyploidy, $n = 12$, $n = 24+$, $n = 36+$.

8. Aneuploidy was discovered in several species, but was most conspicuous in *Phascum cuspidatum* var. *americanum,* in which two races presented the chromosome numbers, $n = 26$ and $n = 29$–30.

9. So-called accessory chromosomes were found in more than 25 per cent of the species studied. As they differ from normal bivalent chromosomes primarily in their small size and generally precocious disjunction, they were included in the chromosome counts. These minute chromosomes were found only in species that appear to be polyploid.

10. Larger, heteromorphic bivalent chromosomes, assumed to be sex chromosomes, were seen in several species.

11. Multiple association of chromosomes was found in the first meiotic division of several species whose chromosome number indicates their intrinsic polyploidy. Other cytological evidence for polyploidy was the precocious division of first anaphase chromosomes into two or rarely four parts.

12. Precocious disjunction of bivalents was not infrequent, but very rarely involved all bivalent chromosomes.

13. Species of mosses are concluded to be completely comparable to those of higher plants. Speciation in populations of mosses appears to be governed by the same chromosomal behavior patterns, and perhaps at an even higher rate.

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